School of Molecular and Life Sciences

Living on burrowed time: mygalomorph spiders in Perth city

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Abstract

The world of invertebrates represents a void of knowledge. In **Chapter 1**, I introduce the major problems in invertebrate conservation relating to short-range endemism, urban environments, and the aims of my thesis.

In **Chapter 2** I introduce the concept of 'trait surrogacy' and define it as '*the use of a chosen species to demonstrate a collective response in other taxa due to shared, functional characteristics'*. Trait surrogacy is a novel term that may be broadly applicable throughout conservation biology. All taxa are limited by space, time and resources. I hypothesise which traits might be most influential in niche partitioning and use examples to demonstrate convergences in life strategies across taxa. In terms of conservation, I suggest that trait surrogacy may be applied to rare, cryptic and unknown taxa. Through trait surrogacy I extend studies on mygalomorph spiders in urban areas to include other short-range endemic taxa, as well as other habitats.

In **Chapter 3** I present a field survey of patches of remnant vegetation within metropolitan Perth, Western Australia to identify the distribution of mygalomorphs in urban areas. I investigate the potential factors influencing presence of mygalomorphs in a patch. Such factors included size of patch, changes in surrounding land-use, invasive weed cover, presence of rabbits and human disturbance. 'Quality' – as defined by degree of effect of disturbances caused by invasive weed, rabbits and humans - was more important than the 'quantity' (size) of the patch. I found weed invasion to be the highest threat to mygalomorph species and other short-range endemics in urban patches.

It has long been supposed that mygalomorph spiders were specialised in terms of microhabitat requirements. But this had not been confirmed. In **Chapter 4** I conduct an experiment to explore whether mygalomorph spiderlings actively choose microhabitats during dispersal, or if microhabitat use is random and species tend to have higher survival in some microhabitats over others. My findings on the detrimental presence of invasive veldt grass (*Ehrharta* spp.) in **Chapter 3**, led me to incorporate veldt grass as a microhabitat option. Of the three species of spiderlings tested, one (*Idiosoma sigillatum*) showed a high preference for veldt grass as a microhabitat. The microhabitat choices of the other two species (*Idiommata blackwalli* and an *Aganippe sp.*) supported the hypothesis that mygalomorph spiderlings make active choices in ground cover when selecting a site for their permanent burrow. The counter-intuitive preference of *I. sigillatum* suggests that an

ecological trap may exist in lower quality habitat. While an ecological trap was present for *I. sigillatum*, the other species tested, as well as potentially other short-range endemics, would be adversely affected by the landscape trap formed by an increase in veldt grass. Veldt grass may also add to the fuel load and increase the fire proneness of remnants in the Perth metropolitan area.

In **Chapter 5**, I consider how season may affect predation on different mygalomorph species. At different times of the year, depending on the species, male spiders leave the safety of their burrow to roam and find a female to mate. During summer, a large (5 cm) species (*Aname mainae*) roams, but during winter many smaller species (3 cm) roam. I aimed to determine if size of spiders and/or if the season influenced frequency of predation. With the use of clay models, I found that, although predation risk was high, spider size and dispersal season did not significantly influence predation, except of that by wasps. However, since these wasps were co-evolved specialists, I conclude that it is unlikely that they are a threat to mygalomorph persistence in urban areas.

In **Chapter 6** I present data on monitoring the survival and response of mygalomorph spiders after both high and low intensity fires. While mygalomorphs are initially well protected in their burrow even during intense fires, spiders may be left vulnerable to predation or be otherwise compromised after fires. Few studies describe the effect of fire on mygalomorph spiders, and none have been conducted in urban areas, where fire intensity and frequency, post-fire disturbance and level of predation may differ significantly from non-urban areas. Some spiders relocate a short distance (< 1 m) in post- low intensity burn conditions. I therefore explored risk of predation for such dispersing individuals in burn areas compared to adjacent unburnt areas. Using plasticine spider models, I found that predation in burnt areas was significantly higher than in unburnt areas. My data suggests that intense fires may represent a severe threat to mygalomorph spiders in urban areas. I considered the mobility and dispersal characteristics of other short-range endemics and concluded that fire may be especially detrimental to such taxa in urban areas in terms of re-colonisation of patches and management.

In **Chapter 7** I discuss how my thesis chapters synthesise to form a coherent depiction of threats to mygalomorph spiders, and other short-range endemics in urban areas. My project fits into the broader scheme of invertebrate conservation by providing logical reasoning and scientific evidence to support claims and conclusions. Future directions and limitations are highlighted, as are the need for enhanced science communication and advocacy in invertebrate conservation.

Declaration by author

My thesis contains no previously published or written by anyone other than myself, except where cited or acknowledged in contributions by others. I am primary author of all chapters and published manuscripts but have clearly stated the contribution of others of works included in my thesis. A summary table has been provided stating specific contributions of authors in terms of writing, editing, study design and statistical analysis.

All content has been the product of work carried out since the commencement of my research higher degree candidature. This thesis has not been submitted partially or in full to any other university or tertiary institution for the qualification of any other award or degree.

I acknowledge that copyright of all my thesis content resides with the copyright holder, Curtin University, and will be made available immediately for research and study in the University Library.

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Lastly, and with great candour, regrets to all the spiders sacrificed in the name of science – I hope your deaths will not be in vain.

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List of abbreviations used

ANOSIM	Analysis of Similarities
EPA	Environmental Protection Agency
HIREC	Human-induced Rapid Environmental Change
IUCN	International Union for Conservation of Nature
MCAO	Monte-Carlo Attributes in an Ordination
MDS	Multi-Dimensional Scaling
MST	Minimal Spanning Tree
PCC	Principal Component Correlation
RTU	Recognisable Taxonomic Unit
SRE	Short-range Endemic
SSH	Semi-strong Hybrid
SWA	South Western Australia
WAM	Western Australian Museum

Definitions of common terms

Short-range endemism:	Distribution of a species is with 10 000 km^2, traits of low mobility, low dispersal, low fecundity and high specialisation.
Mygalomorph:	A type of spider considered basal, having retained two-pairs of book lungs and para-axial fangs.
Biodiversity hotspot:	Region of global biological richness that has lost at least 70% of the original habitat.

Chapter 1

Introduction

"If we and the rest of the back-boned animals were to disappear overnight, the rest of the world would get on pretty well. But if invertebrates were to disappear, the world's ecosystems would collapse"

~ Sir David Attenborough, Life in the Undergrowth (BBC)

1 Introduction

1.1 A sizeable problem

Conservation biology is a relatively new discipline, derived from an increased awareness of how humans detrimentally impact the natural world (Hunter Jr 1996). Conservation biology may address issues concerning species extinction and maintenance of natural biodiversity or ecosystem functioning (Kuussaari *et al.* 2009). As with any initiative, conservation biology is limited by time, effort and resources (Di Marco *et al.* 2017). However, there are large biases towards the conservation of some species over others. Charismatic species generate more funding (resources) and/or receive more attention in conservation management outcomes (effort) (Bulte and Van Kooten 1999; Krause and Robinson 2017). Time is running out for many species, but proportionally, the highest loss of biodiversity through extinction is represented in the smallest species – the invertebrates (Kim 1993; New 1995; Yen and Butcher 1997).

Conservation of invertebrates - despite their overwhelming contribution to biodiversity by representing approximately 80% of all species – does not receive similar proportions of resources or effort as more charismatic species. Seven impediments to effective invertebrate conservation have been identified (Table 1.1) (Cardoso *et al.* 2011).

Table 1.1: Seven impediments to effective invertebrate conservation. Adapted from Cardoso et al. 2011

Term	Definition
Public dilemma	Invertebrates and their ecological services are mostly unknown to the general public.
Political dilemma	Policy-makers and stakeholders are mostly unaware of invertebrate conservation problems.
Scientific dilemma	Basic science on invertebrates is scarce and underfunded.
The Linnean shortfall	Most species are undescribed.
The Wallacean shortfall	The distribution of described species is mostly unknown.
The Prestonian shortfall	The abundance of species and their changes in space and time are unknown.
The Hutchinsonian shortfall	Species ways of life and sensitivities to habitat change are largely unknown.

1.2 Current investments

1.2.1 A wealth of knowledge unearthed

These impediments identified by Cardoso et al. (2011) have led to discrimination against invertebrates in allocation of time, effort and resources for their conservation management. Focusing on endemism or uniqueness of invertebrate representatives may be one way to 'sell' invertebrates to the public (Meuser, Harshaw, and Mooers 2009). Laws in Australia prohibit allowing species to go extinct (EPA 2009), and these laws have been used effectively by invertebrate conservationists to make politicians aware of conservation problems, particularly related to the mining industry (Ecologia 2009; Harvey *et al.* 2011; DSEWPC 2013). Investment sourced from the mining industry has led to an increase in taxonomic knowledge and concomitant increased funding from other sources towards invertebrates, and especially those with distributions known to be highly restricted (Eberhard *et al.* 2009). These invertebrates are termed 'short-range endemics' (SREs) and is synonymous with the terms 'narrow-range endemics', 'micro-endemics' and 'restricted range distribution species'. Short-range endemism was defined by Harvey (2002) as taxa with an entire geographic range known to be less than 10 000 km^2 and typically possessing traits of low mobility and dispersal capabilities, low fecundity and high habitat specialisation. Ironically, this form of rarity (Rabinowitz 1981) is a relatively common global phenomenon amongst invertebrate clades. Invertebrate SRE representatives include, but are not limited to: stygofauna, troglofauna, millipedes, schizomids, snails, velvet worms and mygalomorph spiders (Harvey 2002; Harvey *et al.* 2011). However, it is highly likely that the SRE definition extends to many non-invertebrate taxa.

1.2.2 Generally specialists

SREs typically show highly associative and specialised adaptions that have evolved over very large timeframes. For example, troglofauna demonstrate adaptations to life underground such as translucency, reduction in eyesight and increased hairiness (Romero 2011). Although found in many habitat types, we can identify some SRE strongholds as they are often isolated islands or represent strong discontinuity in the landscape e.g. limestone karsts (Christman *et al.* 2005; Clements *et al.* 2006) and granite inselbergs (De Smedt *et al.* 2018). SREs may also occur throughout subdued (Wardell-Johnson and Roberts 1993) and heterogeneous landscapes (Wardell-Johnson and Horwitz 1996) that - at least historically - are old and stable (Mucina and Wardell-Johnson 2011). Anthropogenic influences are pervasive, which means that passive conservation is not enough to safeguard the future for those with such a high investment in a location (Poisot *et al.* 2011). Changes to the niche they occupy through introduction of novel circumstances (such as

invasive species, changed assemblages and fire regimes), may be disproportionately impacting on species with such traits. Active and urgent measures must be taken to ensure persistence of SRE species.

1.2.3 Urban environments

Arguably, the urban setting represents the most highly modified from a once natural environment. Though a relatively recent area of study, much has been done to quantify how non-human species may adapt, avoid or exploit such environments (Kark *et al.* 2007). It can be assumed that the majority, if not all, SRE species would not be able to adapt or avoid such modifications due to their specialisation for the former natural environment. Although unable to readily move or disperse to avoid urban areas, they may be able to persist in patches of uncleared urban bushland (Mason, Wardell-Johnson and Main, 2016). Indeed, clearing of bushland in urban areas in Western Australia is occurring at a prolific rate (WWF-Australia 2010; Mason, Wardell-Johnson, and Main 2016) to accommodate an ever-growing population. This means all seven impediments to invertebrate conservation (Table 1.1) are highly problematic and ongoing for urban species.

1.3 My aims

In the under-funded area that is invertebrate conservation, coupled with highly modified urban areas, what options are available to better conserve SREs? An opportunity presented itself as a self-directed PhD project, allowing at least some investment of time, effort and resources to assess threatening processes.

My overall aim is to determine major threatening processes that my impact on mygalomorph spiders, that may be extended to other SREs, in an urban environment.

Unfortunately, the limitations in time, effort and resources represented by such a project means my capacity to adequately assess the impact of *all* SRE species in Perth was also unfeasible. Due to the lifetime investment of Adj. Prof. Barbara York Main, enough is known about local mygalomorph spiders to use as surrogate species for other SRE species that may be present in urban areas. Trait surrogacy is a concept I describe in **Chapter 2** where '*the use of a chosen species to demonstrate a collective response in other taxa due to shared, functional characteristics*.' As SRE species have poor dispersal and mobility, in **Chapter 3** I aimed to determine whether quantity of urban patches was more important than quality. This involved a comprehensive survey of Perth remnant

vegetation patches and quantification of human related disturbances. **Chapter 4** aimed to determine if microhabitat specialisation was random or chosen in mygalomorph spiderlings. As veldt grass (*Ehrharta* spp.) significantly correlated negatively with mygalomorph spider presence in **Chapter 3**, was included as a choice for **Chapter 4**. After discovering veldt grass to be an ecological trap for one species (*Idiosoma sigillatum*), I applied the concept of landscape traps to the other two species tested. Through this, I aimed to highlight the threat invasive grass, and other homogenising processes, may have on SREs. Fire is often considered as a homogenising force and I aimed to understand how fire may be threatening process to mygalomorph spiders in urban areas for **Chapter 5**. Using plasticine models, predation was found to be higher in burnt than unburnt areas of the same patch in **Chapter 5.** I aimed to better understand the potential threatening process of changing assemblages and seasonal behaviour of species that predate on mygalomorph spiders in urban areas for **Chapter 6**.

1.4 Expectations

I expected that many of the findings in regarding mygalomorph spiders throughout my project would be related to their short-range endemic traits. I extended the short-range traits along the spectra of mobility, reproductive output and specialisation present in all animal taxa in **Chapter 2**. I expected that such traits may separate even closely related species (phylogenetically) due to contextual differences based on time, space and resources. In **Chapter 3**, I expected that when SRE traits were applied to urban areas, that their poor dispersal and mobility may allow them to persist in even small reserves. I expected that spiderling dispersal was random in **Chapter 4.** I reasoned that any specialisation in microhabitat may have arose from limited capacity to move beyond the microhabitat of the mother. Due to a lack of mobility, low metabolic rates (Mason *et al.* 2013) and burrowing capacity, I also expected the response of mygalomorph spiders to fire in **Chapter 5** to be passive endurance. I also expected that there may be opportunistic predation on spiders following a burn. Similarly, in **Chapter 6** I expected that predation on spiders would show seasonal effects and perhaps more occurring in summer when prey was scarce. Also, that larger spiders may be more highly predated by simply being more visible.

As the following chapters have been prepared for submission for publication, please expect many redundancies in the definition of terms and topics. Impact statements and abstract art have been included as forms of science communication for each chapter to enhance understanding (and enjoyment) while reading this thesis.

Chapter 2

Species trait surrogates to conserve the nameless

"Advocates for a single line of progress encounter their greatest stumbling block when they try to find a smooth link between the apparently disparate designs of the invertebrates and vertebrates."

~ Stephen Jay Gould (1941 - 2002)

2 Species trait surrogates to conserve the nameless

2.1 Impact Statement

We may groove, move, boom
Same strokes for different folks
Time, space and needs unite

2.2 Graphical abstract

2.3 Abstract

Invertebrates are the largest contributors to biodiversity, but current taxonomic impediments inhibit their protection. We suggest an alternative trait-based approach to facilitate conservation of rare, cryptic, difficult to survey, undescribed or unknown taxa. Here, 'a trait surrogate' is defined as '*the use of a chosen species to demonstrate a collective response in other taxa due to shared, functional characteristics*.' We employ taxa representing a wide array of clades and niches to demonstrate how time, space and resources influence functional traits and potential application of trait surrogates to non-invertebrate taxa. Categories of traits relating to high mobility (*movers*), reproductive output (*boomers*) and specialisation (*groovers*) are suggested when considering species traits, surrogates and threats. A case study demonstrates the value of mygalomorph spiders as trait surrogates for short-range endemics in urban areas. Contextualisation based on the limitations imposed by space, time and resources is necessary when considering the potential threats to species.

2.4 Introduction

Conservation biology attempts to maintain biodiversity through the reduction of extinctions (Soulé 1985). Historically, multiple approaches have been used to protect the largest number of species within the limitations of time, effort and resources (Caro 2010). Worthiness of taxa to be conserved has typically been judged by the charisma of species (Colléony *et al.* 2017; Krause and Robinson 2017), because people are more willing to invest in their management (Kontoleon and Swanson 2003). 'Flagship' focal species exemplify species receiving investment disproportionately to the biodiversity that they represent (Bowen-Jones and Entwistle 2002). However, many argue that the benefits of flagship species are their ability to engage the public in conservation efforts and, by default, these species become 'umbrella' species where the conservation of one species leads to the conservation of many other taxa (Lambeck 1997; Clark and May 2002). Similarly, ecosystem processes and functioning may also be protected through conservation of species that have significant impact on many other species. This may be achieved either through the focus on biological interaction (keystone) or through provision of habitat (foundation) (Simberloff 1998; Ellison *et al.* 2005).

More recently, broadly defined 'indicator' species have been used as proxies for biodiversity or environmental changes (Caro 2010; Hunter Jr *et al.* 2016) and are often small or less charismatic species of invertebrate (Eaton *et al.* 2018). Unfortunately, invertebrate indicator species are not

usually considered for conserving other invertebrates, but rather are used to gauge 'quality' of an ecosystem (Caro 2010). Nevertheless, invertebrates constitute approximately 95% of all animal species (Cardoso *et al.* 2011; Mora *et al.* 2011).

Conservation of invertebrate species is important in its own right, in addition to its contribution towards maintaining biodiversity and healthy ecosystem functioning (Wilson 1987; New 1999; Cardoso *et al.* 2011). However, there are many challenges for invertebrate conservation and taxonomic impediments remain among the greatest obstacles to quantifying impacts of environmental threat (Cardoso *et al.* 2011). Criteria for nominating threatened species through agencies such as IUCN require sufficient data for evaluation. Through the efforts of taxonomists, approximately 1.9 million species have been described worldwide, with about 1.4 million of these being invertebrates (Chapman 2009), yet there are still vast numbers of undescribed species. There are also profound limitations in time, effort and resources available for taxonomy. Thus, by default, many taxa are not only name-deficient, but also deficient in the data that would allow assessment of their extinction risk. However, we do know that some clades share functional traits that may limit their response and capacity to accommodate threats to their persistence. For example, many distantly related invertebrate clades (some snails, millipedes and trapdoor spiders for example) can all be considered short-range endemics' (SREs) based on shared traits of low mobility, poor dispersal capacity and low fecundity, resulting in small distribution ranges (Harvey 2002).

Currently, the earth's biota is experiencing a mass, human-induced extinction (Sahney and Benton 2008; Chapman 2009). It is beyond doubt that large numbers of invertebrates have gone extinct without being described or recorded. We know that there are many unrecorded taxa, in much the same way that we know a tree will still fall in a forest even if there is nobody there to witness it. How might we protect those numerous nameless taxa from falling into extinction? We suggest here that one way is through the application of 'trait surrogates' – using shared traits from described, accessible species to deduce response to threats, and then estimating responses for rare, cryptic, difficult to survey, or unknown taxa based on shared traits with the former. As we suggest that trait surrogates can also be applied to include non-invertebrate taxa, so we define it as '*the use of a chosen species to demonstrate a collective response in other taxa due to shared, functional characteristics*.'

What categories of traits are likely to be useful when selecting a trait surrogate? All organisms have limitations in space, time and resources and have developed responses (functional traits) that vary accordingly (Buchmann *et al.* 2008). Here we outline current trends surrounding trait-based

approaches, and demonstrate how trait surrogates may be broadly applied, based on an assessment of well-known taxa from a wide range of clades and niches. We use numerical taxonomic approaches to demonstrate how traits can separate taxa, including those closely taxonomically-related, and provide hypothesised axes for species trait spectrums. We then discuss how species trait spectrums can be used to assess likely surrogates for environmental threat. Finally, we demonstrate a specific application of this concept by outlining a case study on how mygalomorph spiders have been used to assess threatening processes for other SREs in urban bushland.

2.5 A traits-based approach

Trait-based approaches have been used to quantify the niche or functioning of taxa in ecosystems (Buchmann *et al.* 2002; Webb *et al.* 2010; Van den Brink *et al.* 2011). For conservation of species, trait-based approaches have often been restricted to analysis within clades, for example elasmobranchs (Denney, Jennings, and Reynolds 2002; Dulvy *et al.* 2008). Traits could be a useful and consistent approach to assess and prioritise species across taxonomic boundaries for conservation due to a shared response to threats. However, traits may or may not be related to, or be representative of, phylogeny; for example, niche partitioning dictates that natural selection generates traits that enable divergence in lineages (Armstrong and McGehee 1976). Thus, for trait-based approaches, convergent evolution is more important than is divergent evolution (Bevilacqua et al. 2012).

Since, taxa with convergent traits occur globally, trait-based studies that observe responses of taxa to disturbance locally may be globally applicable (Van den Brink *et al.* 2011). Identification of traits and how these traits respond to disturbance or threatening processes is an efficient use of conservation resources at all scales. Conversely, making inferences through shared traits can be imprecise (Van den Brink et al. 2011; Crisp and Cook 2012). However, in the face of time and resource limitations, it may be the most prudent way to assess rare (Rabinowitz 1981), cryptic or unobservable taxa before they go extinct.

To represent the applicability of trait surrogates, we derived an overall pattern of traits and taxa among animals based on the trait profile of 47 taxa. Traits that we selected were likely to be both pertinent to conservation and information was readily available or easily inferred, namely: passive dispersal (without intentional movement), brood size, migration, daily activity responsiveness, and specialisation in abiotic or biotic factors to demonstrate the utility of our approach (see Appendix

9.1 for taxa and corresponding raw values for trait categories). Species were chosen from broad clades that demonstrate vastly different primary life history strategies. For example, three species were chosen from the spider (Araneae) clade but functional traits associated with life strategy diverge.

We used numerical taxonomic approaches (Belbin, 1990) to derive patterns among traits and maintain objectivity. We used the Bray-Curtis Metric to determine degree of association between species. A combination of standardisation (log-1 for eg. 'Brood size' and *[min value/max value]/range* for all variables within the data-set was employed to ensure each variable had a similar influence on the overall pattern. Groups were derived by hierarchical polythetic agglomerative clustering using unweighted pair group arithmetic averaging (UPGMA) with Beta set at -0.1 (see Belbin 2013). To determine influence of groups of trait variables on species groups, we classified the six trait variables using the Two-Step Association Measure (Austin and Belbin 1982), with Beta set at -0.1. We superimposed the species and trait classifications to visualise influence of trait groups on species groups. This formed a two-way table, where each cell corresponds to a species individual trait score (Belbin 2013). If data and analysis were robust, two-way tables were annotated to include darkly shaded (species groups associated with trait groups), and lightly shaded blocks (species groups weakly associated with trait groups).

The validity of cluster analysis can be ascertained using ordination and network analysis, also to detect patterns in the data (Belbin 2013). We presented our distance matrix through semi-strong hybrid multidimensional scaling ordination (SSH MDS, dissimilarity cut at 0.9, Belbin 2013). MDS ordination seeks to provide, in few dimensions, an accurate representation of the similarity between samples (in this case species) using the trait variables. Stress (the difference between input distance and output distance) determined in how many dimensions the ordination can be reliably assessed. We also used network analysis using the minimum spanning tree (MST), the shortest distance travelled to join all species by lines based on the association measure used (in this case Gower), as a further validation. This determines the nearest neighbour (species) to any other species. The three approaches (cluster analysis, ordination, and network analysis) can be inspected visually in one diagram. The greater the congruence between them (i.e., all approaches give similar results), the greater the validity of the categories derived.

We correlated the six variables with the derived groups formed in cluster analysis (non-parametric Kruskal Wallis test). We also assessed whether the derived groups were significantly different from

one another using ANOSIM. Relationships of the 6 variables with the ordination axes were explored using principal axis correlation (PCC procedure in PATN, Belbin 2013). Significance of the correlation of variables to the axes of the two-dimensional ordination derived from the rare species/variable matrix were assessed using randomisation tests (with 10000 permutations) and the MCAO procedure of PATN (Belbin 2013). The direction of variables that were significantly correlated with the ordination axes were plotted on the ordination.

2.6 Outcomes

Numerical taxonomic approaches were used to analyse relatedness between species based on traits from the matrix of raw data. In our analysis this formed groups (Figure 2.1a; cluster analysis), trends (Figure 2.1b; ordination), and networks (Figure 2.1c; Minimum-spanning tree) based on similarity of traits. We found that traits separated even closely taxonomically-related taxa, reliably enabling us to construct trait-based relatedness among species (Figure 2.1).

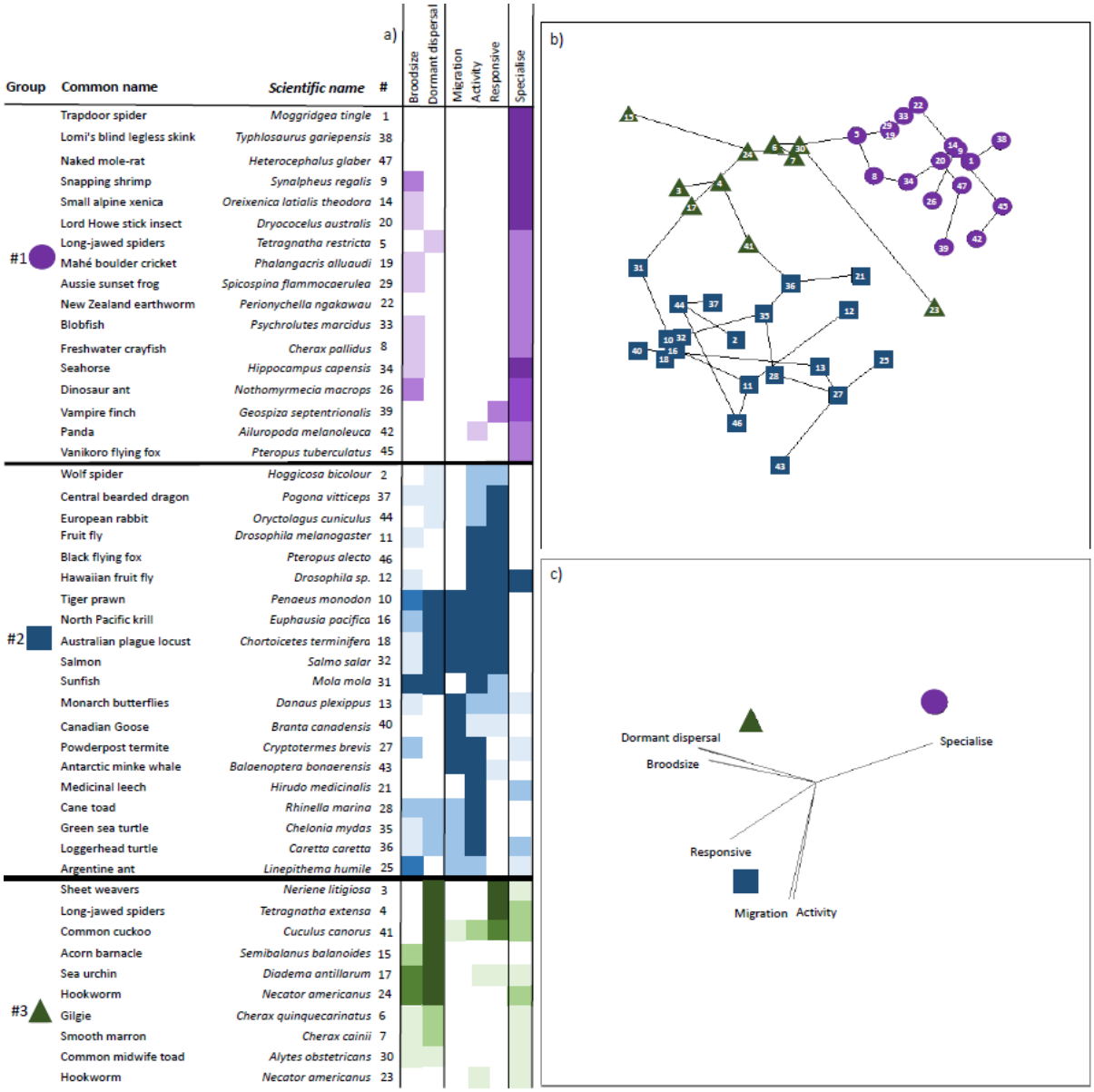


Figure 2.1: Trait-relatedness among selected taxa. Groups were derived by hierarchical polythetic agglomerative clustering using unweighted pair group arithmetic averaging (UPGMA) a) Two-way table overlaying species groups (Bray Curtis Metric, Beta set at -0.1) with trait groups (Two-step Metric, Beta set at -0.1). Darkly shaded cells show species groups that are associated with trait groups, and lightly shaded blocks show species groups weakly associated with trait groups. b) 2D ordination (SSH MDS, dissimilarity cut at 0.9, Stress 0.1903) showing trends among species based on traits; and network analysis (Minimal Spanning Tree - MST) showing minimum distance joining all species with one another. c) Overlays of the six trait variables against the ordination (MCAO, PCC). All variables are significantly ($p < 0.05$) correlated against these axes.

Three distinct groups emerge from the analysis. Typically, Group 1 members showed a high degree of specialisation, but do not have large brood sizes and have low passive dispersal, do not migrate, do not move far during activity and cannot move to respond to change. Exemplars of this group include; trapdoor spider *(Moggridgea tingle*), blobfish (*Psychrolutes marcidus*) and sunset frog *(Spicospina flammocaerulerea*). Group 2 included species that can readily move in response to change, are very active or displayed migration. Few members of Group 2 showed high reproductive output or specialisation in abiotic or biotic variables. Exemplar species include wolf spider *(Hoggicosa bicolor*), Antarctic minke whale *(Balaenoptera bonaerensis*) and Canada goose *(Branta canadenis*). Group 3 included species with large brood sizes, high dormant dispersal but low capacity to respond to change, low activity, no migration and low specialisation. Exemplars from this group include sheet-weaving spiders *(Neriene litigiosa*), acorn barnacles (*Semibalanus balanoides*) and sea urchins (*Diadema antillarum*).

2.7 Traits: an investment for life

Our results support recognition of three broad trait categories that influence the similarity of life; 1) mobility, 2) reproductive output and 3) specialisation. For more effective future science communication of this concept, we coin terms for those species that represent the extremes of each respective trait category as *groovers* (high specialisation), *boomers* (high reproductive output) and *movers* (high mobility).

2.7.1 High specialisation: Groovers

In old, stable landscapes (Mucina and Wardell-Johnson 2011) low reproductive output and mobility may be advantageous to survival, particularly when considering habitat specialisation. If a species becomes well-adapted or specialised to a specific set of environmental parameters, thus falling into the *groovers* category, populations can thrive within those parameters. Venturing beyond those limits through dispersal and mobility is likely to provide diminishing adaptive returns. Habitat specialisation takes evolutionary time and resource variety so that grooves can have established niches within space limitations. Specialisation results in enhanced competitive ability for a particular resource, thus excluding other species from establishing (Rainey and Travisano 1998).

Habitat specialisation is closely allied with endemism in that both acquire selection pressures over time as well as during prolonged periods of isolation (Rabinowitz 1981). However, speciation (Darwin 1859) need to be contextualised within the natural history of the area. Old, (previously) stable landscapes such as those in south-western Australia (SWA), host a biota with high

endemism. When coupled with high levels of threat, such landscapes are classed as global biodiversity hotspots (Myers *et al.* 2000). Accumulation of biodiversity requires slow and/or patchy change over a long timeframe (Hopper and Gioia 2004). For example, SWA has experienced periods of climatic change coupled with subsequent diversification and radiation of taxa (Hopper and Gioia 2004; Rix *et al.* 2015), and small pockets acting as refugia (Wardell-Johnson and Roberts 1993). Some may be dynamic, generating microrefugia within refugia (Tapper *et al.* 2014). Such refugia may host many SRE species as they specialise with the groove. Island species experience the same restrictions in space over time and surviving species therefore tend to specialise on the available resources - increasing efficiency of uptake - to be competitive (Mucina and Wardell-Johnson 2011). It is these areas that require prioritisation in management against rapid human-induced environmental change (Sih, Ferrari, and Harris 2011) and homogenising processes (Mason, Bateman, and Wardell-Johnson 2018). Groovers, by extension, due to their traits may be considered under high threat of extinction in such areas that are undergoing rapid change such as urbanisation (Williams *et al.* 2005).

2.7.2 High mobility: Movers

Mobility, as a species trait, is complex and varies markedly amongst taxa (Doherty and Driscoll 2018). The major driver of mobility may be related to resource acquisition over space and time. For conservation purposes, it may be useful to focus on traits within clades. This could reveal biological trends, such as with Darwin's finches (Mucina and Wardell-Johnson 2011) and could be used more broadly to determine species at high risk of extinction, such as migratory birds (Runge *et al.* 2014; 2015). It is illogical to determine global biodiversity trends by extrapolating from one clade, especially where representatives vary markedly in mobility, such as has been previously demonstrated with birds (Orme *et al.* 2005). However, the comparison of mobility capabilities within one clade can be used effectively in quantifying threatening processes, such as effects of fragmented landscapes on butterflies (Thomas 2000) or freshwater fish (Carvajal-Quintero *et al.* 2017). Mobility is an important trait for conservation as it can make the difference between escaping a threatening process or being consumed by it (Mason, Bateman, and Wardell-Johnson 2018). A species mobility capacity can perhaps act as a predictive trait for the assessment of conservation status in relation to present threats.

2.7.3 High reproductive output: Boomers

High fecundity and dispersal capacity can overcome constraints on mobility in furthering the distribution of a species, particularly sessile or sedentary species (Sorte *et al.* 2018) and/or non-

social species (Mullon, Keller, and Lehmann 2018). High dispersal traits enable some species to recover quickly after disturbance (Kaiser *et al.* 2018). Conversely, a low dispersal ability may make species vulnerable following disturbance (Mason, Wardell-Johnson, and Main 2016) and at risk of extinction if recovery time takes longer than re-establishment (Kaiser *et al.* 2018). Similarly, traits regarding fecundity and lifespan have long been known to affect how organisms thrive under different scenarios, as described by r- and K- selected species (Pianka 1970). High parental care for offspring, shown by K-selected species, is a lengthy time investment. It may be a trade-off against individual survival when there are restrictions on resources or space. Conversely, r-strategists may be hedge-betting against future change by quickly exploiting current circumstances when space and resources are abundant. For example, short generation times may allow for the rapid acclimatisation of species to climatic changes (Peck 2011).

Assessment of threatening processes based solely on taxonomy is not effective (Armstrong and McGehee 1976; Pracheil *et al.* 2016). We support the argument that focusing on traits that make species susceptible or successful under various scenarios can yield more positive conservation outcomes (Pracheil *et al.* 2016) than can taxonomic approaches alone. We support use of complementary approaches for improved conservation outcomes. Choice of trait variables can be expanded as information is gathered on functional traits (Mlambo 2014). Based on the type of traits present in species that we have already categorised broadly, we have framed them along spectrums of mobility, reproductive output and specialisation (Figure 2.2).

We emphasise that the pinnacle of traits of mobility (*movers*), specialisation (*groovers*) and reproductive output (*boomers*), are extreme and that most species will lie to varying degrees along all axes (Figure 2.2). These extremes do not represent those traits that put species most at risk, only that the threats will be different depending on such traits. For example, *movers* like migratory butterflies may be under threat from habitat destruction in multiple countries. Mitigation of this threat would require international policy. Of interest is the case of a *groover* species (a short-range endemic shizomid) whose existence halted an entire mining operation (EPA 2007). These threats are vastly different and thus would require different approaches to resolve. *Mover, boomer* or *groover* traits should not be used to prioritise species for conservation outcomes in themselves. Rather, traits of species must be considered in the context of any potential threats within their distribution. Specifically, how time, space and resources might be compromised to create such a threat specially relating to their traits.

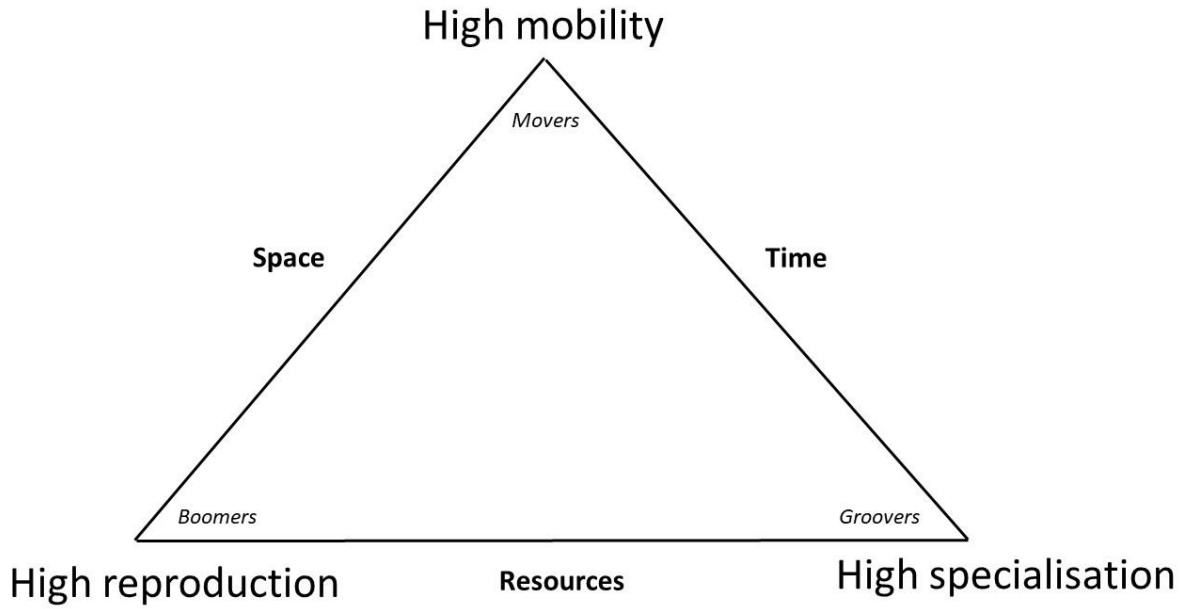


Figure 2.2: Investment in functional traits relating to mobility, reproduction and specialisation will vary based on limitations imposed by space, time and resources. All limitations will be within the bounding regions of space, time and resources depending on the environmental context for the species in question, and similarly the investment in traits will reflect their place somewhere within the triangle. For example, *groovers* have sufficient resources and time, but are limited in space, so they will invest in the place by being highly specialised. Conversely, generalist species do not specialise as they have sufficient space such that mobility and reproduction become more important investments. We would like to stress that *groovers*, *movers* and *boomers* represent extreme investments in traits due to extreme limitation in space, resources and time respectively. Most species will have trade-offs to varying degrees, placing them in different areas within the triangle.

Overall, we consider traits are investments in self, place or future with trade-offs depending on space, time and resources. Species traits will therefor allow us to predict success or threats under different scenarios. It should be stressed that species traits will fall along spectrums and that *groovers, movers* and *boomers* merely represent the most extreme of respective trait investments. We now provide a case study of a *groover* in an urban environment as an example of how trait surrogates may be utilised in conservation biology.

2.8 A case study example: Mygalomorphs as SREs trait surrogates in urban areas

Taxa with an entire geographic range known to be less than 10 000 km^2, with traits of low mobility and dispersal capabilities, low fecundity and habitat specialisation are considered SREs (Harvey 2002). As a term, 'short-range endemism' was first coined by Harvey (2002), but the traits described may also be applicable to 'narrow range' (Ponder 1999) and 'restricted range' taxa (Rabinowitz 1981). Geographic range will naturally vary with biotic (e.g. predator-prey

interactions), abiotic (e.g. seasons, fire), genetic (e.g. inbreeding), anthropogenic (e.g. habitat clearing, invasive species) or a combination of such factors (Mott 2010).

Species' traits that describe short-range endemic (SREs) are likely to be of conservation concern in a (now) rapidly changing environment. Short-range endemism has already been established as representative of a vulnerable trait-based group (Harvey 2002). In the Australian mining sector, guidelines have been implemented effectively in government (EPA 2009) and industry (Callan *et al.* 2011) for priority conservation management and surveying. As an example of how the concept of trait surrogates can be utilised to conserve SREs, we discuss use of mygalomorph spiders as trait surrogates for other terrestrial SREs.

Adequate surveying and management of invertebrates is problematic but essential for conservation and for their contribution to biodiversity and ecosystem functioning. The traits of SRE species confirm these species as being most at threat from a rapidly changing environment. However, SREs are not threatened based on lineage, but rather due to their SRE, or *groover,* traits. Therefore, a non-related surrogate may be better suited to guide the conservation of the many such taxa at risk of extinction. Besides being exceptionally long-lived (Mason, Wardell-Johnson, and Main 2018), mygalomorph spider species represent the quintessential *groovers* as they are sedentary, have poor dispersal capacity, low fecundity (Main 1987; Main 1999; Mason, Wardell-Johnson, and Main 2016; Rix *et al.* 2017) and demonstrate microhabitat specialisation (Mason, Bateman, and Wardell-Johnson 2018). Indeed, they could be considered grooviest of *groovers*. As such, mygalomorph spiders may be used as trait surrogates to demonstrate a collective response of other terrestrial SREs, or *groovers*, to threatening processes or change.

Arguably, urban environments represent the greatest permanent change from a once natural state. They also produce the most intensive human footprint (Venter *et al.* 2016). Habitat clearance, modification and infrastructure represent very rapid change in the context of evolution and adaptability. Due to habitat specialisation, it could be assumed that no SRE species would be able to persist in such an environment. However, patches of remnant vegetation are still maintained within the urban landscape and due to SREs low dispersal and mobility, such taxa may be able to persist even in small patches.

In metropolitan Perth, SWA, patches vary in amount and quality. We found that changes in quality of urban bushland have impact on the persistence of mygalomorph spiders, and by extension other

SRE species (Mason, Wardell-Johnson, and Main 2016). Specifically, we found that homogenisation of the previously heterogeneous environment in the few remaining patches of bushland was a major threat to these *groovers*. Establishment of veldt grass, an invasive weed from South Africa, is a major threat due to its pervasive and destructive traits that results in a monoculture (Mason, Bateman, and Wardell-Johnson 2018). This homogenisation processes poses not only a threat to mygalomorph spiders, but all other *groovers* that rely on and specialise within niches of the previously heterogenous landscape. As a considerable number of *groovers* can exist in a small area, the implications are dire for biodiversity loss and extinctions.

Use of mygalomorph spiders as trait surrogates for other *groovers*, provides better understanding of potential threats that can be present in their environment. The extinction crisis highlights the need for adoption of trait surrogates as a crucial tool in the conservation biology toolkit to better protect the unknown, unloved and unkempt from the profligacy of humanity.

2.9 Conclusions

While change is constant, type and rate of change is not. Current rates of change urge convergence on a future approach to conservation that protects all biodiversity. We suggest that greater opportunities for conservation arise from complimentary use of traits surrogacy with taxonomy during this time of diminishing resources. Securing a synthesis of these approaches may enable focus on vulnerable species, before the world is rendered without the splendour represented by species such as the blobfish.

Chapter 3

Quality not quantity; conserving species of low mobility and dispersal capacity in south-western Australian urban remnants

"Quality is not an act, it is a habit."

~ Aristotle (384BC - 322BC)

3 Quality not quantity; conserving species of low mobility and dispersal capacity in south-western Australian urban remnants

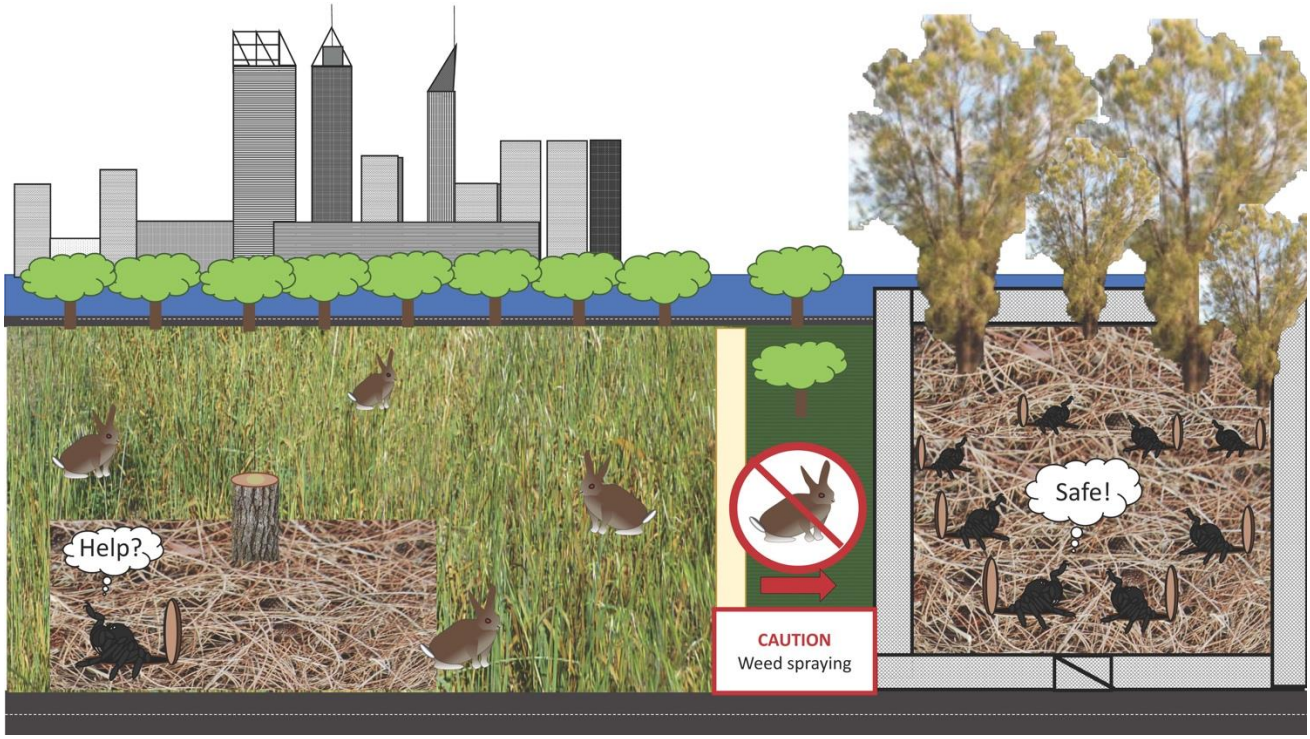
3.1 Impact Statement

City bush, our home

Don't need much space, only care

Keep out invaders

3.2 Graphical abstract



3.3 Abstract

Urban remnant vegetation is subject to varying degrees of disturbance that may or may not be proportional to the size of the patch. The impact of disturbance within patches on species with low mobility and dispersal capabilities was investigated in a survey targeting nemesiid species of the mygalomorph spider clade in the Perth metropolitan area, south-western Australia. Nemesiid presence was not influenced by patch size, but presence did negatively correlate with higher degrees of invasive grass and rabbit disturbance. Further, patch size was significantly positively correlated with degree of disturbance caused by rabbits. Compared to quadrats, patches were not as effective as sample units in determining the impact of disturbance on nemesiid presence.

3.4 Introduction

Conservation biology focuses on identifying factors or patterns that pertain to biodiversity persistence and survival (Gilpin and Soulé 1986; Schulze and Mooney 1994); with higher quality environments increasing chances of survival (Thomas *et al.* 2001). Size of suitable habitat is important to support viable populations (Shaffer 1981; Gilpin and Soulé 1986). Measuring quality and size of habitats is especially important for conservation practises as it allows appropriate population or species management to be implemented (Shaffer 1981). Disturbance within patches can be influenced by surrounding land-use, patch size and patch shape (Pickett and White 1985). Maintenance of at least the minimum required size and quality of habitats will increase probability of persistence for viable populations (Shaffer 1981; Gilpin and Soulé 1986). Required habitat of native species within an urban matrix is usually confined to remnant patches, depending on species and degree of specialisation. Urbanisation is a relatively recent process in Australia. Therefore, associated threats are novel for native species persisting in urban areas. Identifying factors or patterns important for conservation purposes allows implementation of more informed management practices (Olson *et al.* 2001).

Informed conservation management is especially important in the South-west Australian Global Biodiversity Hotspot (SWA). The biota of SWA is therefore globally significant (Hopper and Gioia 2004; Rix *et al.* 2014), but also threatened (Klausmeyer and Shaw 2009; Wardell-Johnson, Keppel, and Sander 2011). Though invertebrates were not included in Myers *et al.* (2000) criteria, evidence supports invertebrate biodiversity as also being proportionally high within SWA (Crisp, Dickinson, and Gibbs 1998; Main 2001; Harvey *et al.* 2011). Many clades of invertebrates are locally endemic

to the region (Rix *et al.* 2014), likely attributable to shared life history characteristics. A species or clade may be considered a short-range endemic (SRE) if they have a distribution range of less than 10 000 km^2, low fecundity, low dispersal and low mobility. Recently, recognising short-range endemism has allowed rapid synthesis of conservation protocols for a large group of previously unprotected species in SWA (Harvey 2002; EPA 2009; Harvey *et al.* 2011).

Many species of mygalomorph spider are considered SREs. However, taxonomic impediment, taxonomic resolution and insufficient information means SRE status cannot be assigned for the entire mygalomorph clade, hindering conservation outcomes (Mace 2004). Population counts of mygalomorphs may be misleading as to the viability of some populations, due to slow maturation, cryptic mating systems and long lifespans (Main 1987; Abensperg-Traun, Smith, and Main 2000). For example; *Gaius villosus* mature at approximately 5 years for females and 3 years for males (Main 1984). Males die after their mating season. However, some females can live up to 43 years (Main 1987; Abensperg-Traun, Smith, and Main 2000; Mason, Wardell-Johnson, and Main 2018). Persistence despite small population size has occurred after genetic bottlenecks (Main 1987; Abensperg-Traun, Smith, and Main 2000). This implies that limited dispersal and longevity could enable mygalomorphs to persist in small, isolated populations indefinitely. This may also apply to other long-lived SRE taxa such as cossid moths (Cossidae) and some Coleoptera (e.g. Curculionidae) (Abensperg-Traun, Smith, and Main 2000; Harvey 2002). Unfortunately, being long-lived also increases the likelihood of ghost populations; aging populations that can no longer recruit and are therefore not viable.

Thomas (2000) concluded that species either with high or low mobility, are less impacted by habitat fragmentation than those with intermediate mobility. Mygalomorph spiders are generally sedentary, except for roaming males. Their poor dispersal ability may mean they require less area in which to persist indefinitely (Main 1987; Abensperg-Traun, Smith, and Main 2000). Thus, persistence of mygalomorphs in urban areas may be more dependent on the quality rather than absolute size of the remaining habitat. This claim is further substantiated by work on mygalomorph populations persisting in remnant vegetation of less than 20 hectares in 'the wheatbelt', agricultural land near Tammin, WA (Main 1987). As few as twenty *Gaius villosus* matriarchs (females that have reproduced at least once) are thought to be capable of sustaining a viable population indefinitely, if they are near one another (Main 1987). More than twenty matriarchs can occur in less than 10 000 m^2 in these wheatbelt populations (Main 1987).

The overall aim of this study was to determine the likelihood of persistence of mygalomorph populations in urban remnant vegetation of the SWA. We examined the effects of urbanisation on mygalomorph spiders, using nemesiids as indicator species, in remnant patches of native vegetation of the Perth Metropolitan Area, Swan Coastal Plain. Nemesiidae is a family of mygalomorphs, with ten genera and one hundred and four described species occurring in Australia (Framenau, Baehr, and Zborowski 2014). Nemesiids generally have an open (no lid) and conspicuous burrow. If size of remaining habitat was not a threat, then it becomes important to identify other threatening processes within remaining habitat. In particular:

i) *Does change of surrounding land-use correlate with disturbance variables in urban remnant vegetation patches?* Based on low mobility, we expected surrounding land-use to not correlate strongly with nemesiid presence or with disturbance variables.

ii) *Do disturbance variables correlate with patch size and/or nemesiid species presence?* We expected disturbance variables to negatively correlate with presence of nemesiids and patch size. However, patch size was not expected to correlate with nemesiid presence.

3.5 Methods

3.5.1 Study site

Perth experiences a Mediterranean climate, with a mean annual rainfall of 740 mm (Australian Bureau of Meteorology, 2011), although this has been trending lower since 1970 (Bates *et al.* 2008). Approximately 80% of rainfall occurs in the winter months with only 4% occurring in summer (Australian Bureau of Meteorology, 2011). Soil of the Spearwood dune system is well-drained and highly leached pale yellow quartz sand, formed in the mid- to late Pleistocene (Kendrick, Wyrwoll, and Szabo 1991). Major soil types were found to correlate with significant change in spider assemblages on the Swan Coastal Plain (Lacey 2012), so sites for this survey were selected to the west of the Bassendean dune system.

3.5.2 Field survey

Comprehensive surveying was required to confidently determine the distribution of nemesiid spider species. Earlier studies used pitfall traps (Harvey *et al.* 1997) that capture specimens not necessarily directly associated with a specific location. Typically, it is only the males that are trapped as they roam to find a mate once sexually mature, and perish shortly thereafter (Main 1984). Due to the potentially high mobility of males, they may be trapped a considerable distance from where

they left their burrow. We used a targeted survey approach to determine the number of known locations where nemesiids occur (Olson, Van Norman, and Huff 2007). This was considered the most effective method given the primarily sedentary lifestyle and poor dispersal of mygalomorph species (Harvey *et al.* 2011). Using a targeted approach by locating burrows, enabled more precise information on the distribution of nemesiid species and potential urbanisation threats to be gathered.

A stratified random approach was used whereby a mosaic of habitats was targeted and surveyed, but the transect grid is otherwise random. Sampling was designed by nesting one hundred and thirty-six 100 x 100 meter quadrats divided into ten 100 m transects spaced 10 m apart (Figure 3.1) within forty-one patches of remnant native vegetation (Figure 3.2). Randomisation was achieved using the 'Random points' function in the program QGIS v2.8.1 Wein, where each point was the centre of the quadrat. If the point was too close to the boundary, it was shifted in until the quadrat fit within remnant vegetation. Similarly, if points were so close that quadrats overlapped, they were moved apart to the shortest distance to where they would no longer be overlapping. Quadrats were uploaded onto a Garmin handheld GPS and surveyors recorded burrows within 5 m either side of the transect line they were traversing. Due to health and safety risk, surveying was always completed with at least one other person. Quadrats in dense, impenetrable vegetation (e.g. stands of prickly moses, *Acacia pulchella*) were replaced by alternative random sites in the interests of volunteer safety.

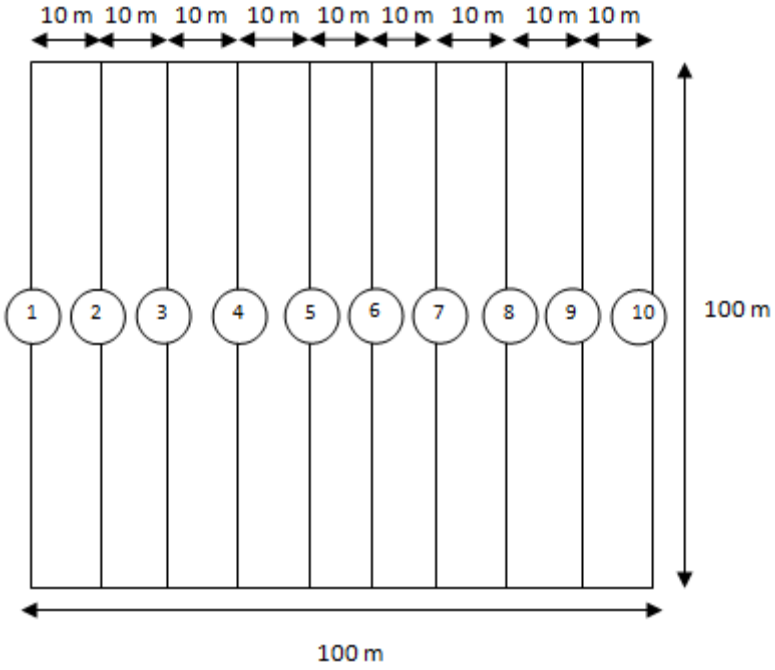


Figure 3.1: Sampling design of mygalomorph targeted survey. Ten transects (1-10, circled), spaced 10 m apart within 100 m x 100 m quadrats. One hundred and thirty-six quadrats were nested, using a randomising mapping function, throughout 41 remnant vegetation patches within urban areas of Perth, Western Australia.

Site #	Area (ha)	Site name
1	1.5	Hently Loop
2	1.6	Rufus Parkway
3	2.1	Natalie Way
4	2.7	Balcatta Park
5	3.0	Cadogan Street
6	3.2	Goldworthy Ent
7	3.3	Glenbar Road
8	3.6	Amstel Park
9	4.5	Conference Green
10	4.9	Padbury Park
11	5.0	Floreat Park
12	5.1	Paloma Park
13	5.9	Montrose Park
14	6.2	Padstow Street
15	6.7	Hollywood Reserve
16	8.0	Pinnaroo Valley
17	12.3	Coolbellup Reserve
18	13.0	Point Walter Reserve
19	13.6	Gibson Park
20	14.2	Woodvale Reserve West
21	14.3	Highview Park
22	14.5	Sir Fredrick Samson Park
23	15.3	Sheperds Bush Conservation
24	16.4	Yorston Place
25	16.5	Landsdale Park
26	28.1	Bibra Lake Reserve
27	28.2	Shenton Park Bushland
28	28.5	Hepburn Heights Conservation
29	34.1	Marangaroo Conservation
30	36.0	Woodvale Reserve East
31	40.4	Wireless Hill Park
32	48.2	Piney Lakes
33	48.6	Bibra Lake Park
34	49.1	Craigie Bushland
35	82.0	Warwick Open Space
36	101.2	Star Swamp Bushland
37	104.0	Manning Park
38	133.0	Trigg Bushland
39	134.1	Koondoola Bushland
40	358.8	Kings Park
41	426.9	Bold Park

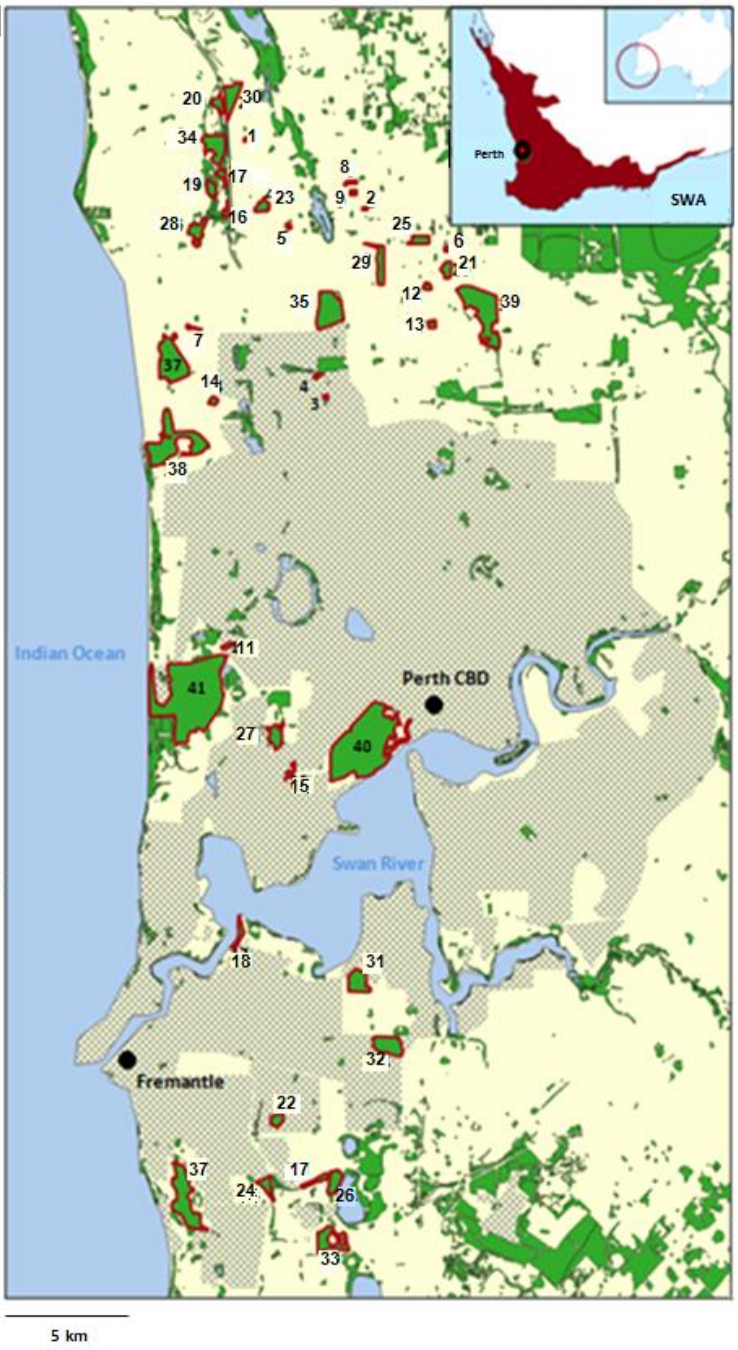


Figure 3.2: Perth metropolitan urban extent (light yellow), and extent in 1965 (grey hashing), with native remnant vegetation (green) patches surveyed (red border) ordered (Site #) from smallest area (1) to largest area in hectares (41). Cities of Perth and Fremantle are also marked (black dots). Map generated using Geographic Information System version 2.18.14 (http:/qgis.osgeo.org).

3.5.3 Nemesiid observations

Nemesiid spider (Figure 3.3a) burrows (Figure 3.3b) were directly observed, identified, and measured (diameter, diagnostic features; silk lines, number entrances, sand mounds). Burrow locations were recorded using a GPS, accurate to within 5 m. Although other mygalomorph burrows were recorded, statistical analysis was restricted to nemesiids, due to potential for bias arising from the unobserved highly camouflaged burrows in other families. Surveying was also not undertaken during heavy rains. This was because we found that some species of nemesiid pull their burrow opening in on itself during heavy rain. No doubt this enables avoidance of flooding to open-holed burrows, but also make burrows more difficult to observe after heavy rain.

Figure 3.3: a) Nemesiid mygalomorph spider (*Aname mainae*), 55 mm in body length. b) Nemesiid mygalomorph spider burrow (*Aname mainae*), 22 mm in diameter. c) Habitat with low weed invasion; understorey predominantly native species. d) Habitat with high weed invasion; predominantly veldt grass (*Erharta spp.*).

Past records from the Western Australian Museum (WAM) indicate a previously uniform distribution of nemesiids throughout the Perth urban area. They have also been recorded throughout the study area since 1922. Museum records were not used for analysis as very few

included locations that were specific enough to compare to present distributions. All sites in a bushland survey conducted by WAM during 1996-1997 where mygalomorphs were found contained nemesiids as the dominant group collected (Harvey *et al.* 1997). We concluded that nemesiids were appropriate indicator species for a group subject to taxonomic impediment (Harvey *et al.* 2011). It is apparent that more nemesiid species were observed in this survey than have been recorded by the Museum. As such, analysis was here limited to presence and absence until species can be verified by subsequent study.

3.5.4 Variables

Disturbance factors such as; invasive grass cover, rabbit (*Oryctoglagus cuniculus*) and rubbish presence were recorded for each quadrat. Invasive grass cover was chosen as a variable due to the homogenising effect it tends to have on native biodiversity. Rabbits and other diggings were observed to destroy the burrow entrance in previous studies (pers. obs). Rubbish was used as a proxy for human activity within patches.

Invasive grass (Figure 3.3c, d) was estimated as a proportion of quadrat covered where number of 100 m^2 (n) covered was estimated over the 10000 m^2 quadrat (see equation below).

$$Invasive\ grass = \left(\frac{n(100)}{10000} \right)$$

Rabbit presence was calculated as a proportion (< 1) equal to the number of evidence (n), such as droppings or diggings found per 10 m over 100 m transects (t) and warrens (w) adding 0.5 final score (see equation below).

$$Rabbit\ presence = \left(\frac{n(10)}{t100} \right) + \ (0.5w)$$

Rubbish proportion (< 1) was calculated in a similar fashion, with evidence of active bunkers (b, +0.5) and dumping of industrial waste (i, +0.3) heavily influencing calculations (see equation below).

$$Rubbish\ presence = \left(\frac{n(10)}{t100} \right) + \ (0.5b) + \ (0.3i)$$

To account for the possibility of ghost populations in an area of rapid urban expansion (Figure 3.2), change of surrounding land-use was incorporated over a timeframe of fifty years between 1965 and 2015. Surrounding land-use area was measured by generating shapefile layers (buildings [B], roads [R], parkland [PL] and other remnant vegetation [RV]) within 250 m, 150 m and 50 m buffers. Buffers were measured for both patch and quadrats in the open source program Quantum

Geographic Information System (Team 2017). The Nearmap plugin was used to determine the proportion of different land-use within each buffer area. The same methodology was performed for surrounding land-use in 1965 using maps available through SLIP (Shared Land Information Platform) Interrogator+.

3.5.5 Statistical analysis

PATN v. 3.0 (Belbin 2013) was used to analyse patches based on the twenty-four surrounding land-use variables as intrinsic in multivariate analysis. We derived groups of patches with similar measures of surrounding land-use proportions using the range standardised values of the 10 measures described earlier (called 'intrinsic variables', following Belbin (2013) in numerical taxonomic or pattern analysis approaches (Belbin 2013). The key steps were (1) use cluster analysis to identify groups of patches (row groups) that, on the basis of the twenty-four intrinsic variables, are more similar to other members of their groups than to members of other groups, (2) superimpose groups based on the variables (column groups) over the patch groups to identify which variable groups are strongly or weakly represented in different patch groups, and (3) validate the patch groupings by applying different methodologies (MDS ordination and network analysis), to assess congruence between the ordination (for trends), network analysis (for nearest neighbours) and the cluster analysis (for groups). All analyses described below used PATN (Belbin 2013).

The Gower metric was used to determine degree of association between different patches based on surrounding land-use composition to generate groups using unweighted pair group arithmetic averaging (UPGMA) with Beta set at -0.1 (see Belbin 2013). To determine the influence of particular intrinsic variables on patch groupings, we classified the intrinsic variables using the Two-Step association measure with Beta set at -0.1. A two-way table was used to visualise the influence of particular variable groups on the different patch groups, where each cell corresponds to a particular patch score on a particular land-use variable. Shading in the two-way table indicates strength of association between patch and land-use variable. Dark shaded blocks indicate strong associations between groups of patches (sites) and groups of variables, and light or clear blocks indicate weak association.

We presented our original distance matrix visually through semi-strong hybrid multi-dimensional scaling ordination (SSH MDS with dissimilarity cut level at 0.6) (Belbin 2013). MDS ordination seeks to provide, in few dimensions, an accurate representation of the similarity between samples, in this case patches, using the surrounding land-use variables. Stress (the difference between the

input distances and the output distances) determined in how many dimensions the ordination can be reliably assessed. Here, low stress enabled assessment in two dimensions. The Minimum Spanning Tree (MST, Belbin 2013) was used together with SSH MDS to assess congruence between ordination (trends), cluster analysis (groups) and network analysis (nearest neighbour). The three approaches were inspected visually in one diagram. The greater the congruence between them (i.e., all approaches giving similar results), the greater the validity of the derived patterns.

Mygalomorph presence and the disturbance variables; rabbit, weed and rubbish were used as extrinsic factors. Relationships of extrinsic variables to the ordination axes were explored using principal axis correlation (PCC procedure in PATN, Belbin 2013). Significance of the correlation of variables to the axes of the two-dimensional ordination derived from the matrix was assessed using randomisation tests (with 1000 permutations) and the MCAO procedure of PATN (Belbin 2013). Vectors of variables correlated significantly with the ordination axes were plotted. Extrinsic factors were superimposed on a two-dimensional semi-strong hybrid multidimensional scaling ordination (2D; stress 0.16, SSH MDS; dissimilarity cut off level 0.6) to visualise influence of groups on those factors.

ANOVA were used to determine correlations between disturbance variables and presence of nemesiids for both quadrat and patch scale in the Microsoft Excel plugin StatistiXL 1.8 (Withers and Roberts 2007). As multiple quadrats were in many of the patches surveyed, the factors gathered for each quadrat were averaged for each patch. Quadrat and patch factors were analysed separately and then compared to determine which may be the more useful unit of measurement.

3.5.6 Limitations

The number of burrows located within a quadrat varied markedly depending on species. Species naturally vary in population density and abundance. Using total number of burrows was not logical when species status is not yet verified; this was another reason to limit analysis to presence and absence of all nemesiid species. Vegetation type and structure is likely to have an effect on nemesiid presence (Schut *et al.* 2014) and visibility. Degree of vegetation heterogeneity, even within quadrats, was too high to account for in this study. Degree of heterogeneity between patches may be similar, as has been found in agricultural landscapes (Thorbek and Topping 2005), and thus not impact on the findings. As noted by Stenhouse (2004), the management of remnant vegetation is difficult to analyse due to the many different authorities responsible for land management in the Perth

metropolitan area. We therefore excluded from analysis the potential impact of different management authorities on disturbance variables.

Quadrat data were not useful in analysis of surrounding land-use as groups were too ill-defined. This may be explained by many of the quadrats, in larger patches especially, having high proportions of remnant vegetation within the buffer zone. Sampling bias for nemesiid species in patch scale analysis meant that this could not be used as an extrinsic factor. As such, surrounding land-use analysis was limited to using disturbance variables as extrinsic factors. It is worth mentioning that although the study was limited to an urban area, nemesiids are common Australia-wide in uncleared bushland beyond the urban boundary.

3.6 Results

Presence of nemesiid burrows was recorded in nineteen of the forty-one patches, and sixty of one-hundred and thirty-five quadrats. Density of adults (as determined by size of burrow) greatly varied between quadrats, from one to 42 burrows. Recruitment was apparent in the smallest patches examined (Figure 3.2: #4, < 2 ha) with spiderlings and varying age groups present in all but one of the patches (Figure 3.2: #21) where nemesiids were found. Change of surrounding land-use since 1965 did not correlate with nemesiid presence (Table 3.1). Hence, patches that were previously surrounded by intact vegetation did not correlate with nemesiid presence, as would be expected if species were occurring as ghost populations.

Table 3.1: Twenty-four land-use variables used as intrinsic factors in PATN (Belbin 2013) analysis. Code used in Figure 3, is described by Year, Land-use and Buffer size. Minimum, maximum, mean and standard error (SE) of proportions surrounding patches are listed for each variable.

Code	Year	Land-use	Buffer size	Minimum	Maximum	Mean		SE
2015.B.50	2015	Building	50	0	0.58	0.23	±	0.06
2015.B.150	2015	Building	150	0	0.65	0.28	±	0.06
2015.B.250	2015	Building	250	0.06	0.74	0.43	±	0.07
2015.R.50	2015	Road	50	0.04	0.91	0.30	±	0.06
2015.R.150	2015	Road	150	0.05	0.41	0.14	±	0.04
2015.R.250	2015	Road	250	0.08	0.37	0.25	±	0.04
2015.PL.50	2015	Parkland	50	0	0.69	0.19	±	0.06
2015.PL.150	2015	Parkland	150	0	0.45	0.13	±	0.05
2015.PL.250	2015	Parkland	250	0	0.52	0.17	±	0.06
2015.RV.50	2015	Remnant vegetation	50	0	0.61	0.05	±	0.06
2015.RV.150	2015	Remnant vegetation	150	0	0.67	0.07	±	0.06
2015.RV.250	2015	Remnant vegetation	250	0	0.34	0.07	±	0.05
1965.B.50	1965	Building	50	0	0.33	0.03	±	0.04
1965.B.150	1965	Building	150	0	0.48	0.05	±	0.05
1965.B.250	1965	Building	250	0	0.48	0.05	±	0.05
1965.R.50	1965	Road	50	0	0.47	0.07	±	0.05
1965.R.150	1965	Road	150	0	0.48	0.04	±	0.05
1965.R.250	1965	Road	250	0	0.26	0.04	±	0.04
1965.PL.50	1965	Parkland	50	0	1	0.09	±	0.08
1965.PL.150	1965	Parkland	150	0	1	0.08	±	0.05
1965.PL.250	1965	Parkland	250	0	1	0.08	±	0.04
1965.RV.50	1965	Remnant vegetation	50	0	1	0.72	±	0.10
1965.RV.150	1965	Remnant vegetation	150	0	1	0.75	±	0.10
1965.RV.250	1965	Remnant vegetation	250	0	1	0.79	±	0.09

3.6.1 Change of surrounding land-use affect disturbance and nemesiids

Intrinsic factors formed distinct groups, and two extrinsic factors were found to be significant: size of patch and rubbish (Figure 3.4 and 3.5).

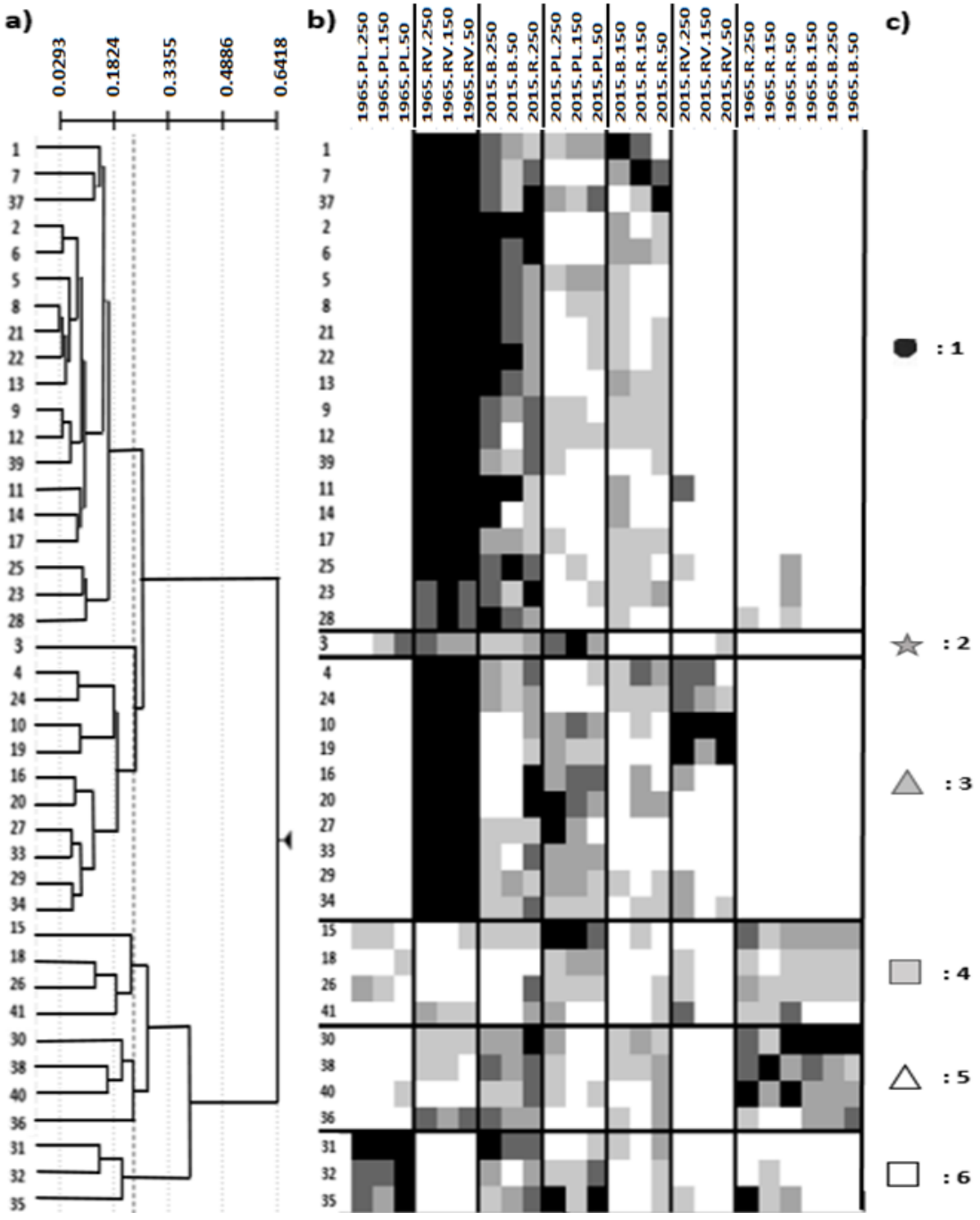


Figure 3.4: (a) Dendrogram showing line along which groups are formed as dark dashed line that corresponds to groups shown in two-way table. (b) Two-way table showing 6 groupings of 41 patches during 2015 and 1965 using proportion of land-use variables (R: Road, PL: Parkland, B: Buildings and RV: Remnant Vegetation) at buffers of 250, 150 and 50 m. Dark shaded blocks indicate strong associations between groups of patches and groups of variables, and light or clear indicate weak association. Codes for land-use variables columns in (b) correspond to Table 3.1. Gower (rows), Two-step (columns), UPGMA. Group symbols and numbers (c) correspond to Figure 3.4 and numbers in text whereas patch numbers (1-41) correspond to patches shown in Figure 3.1.

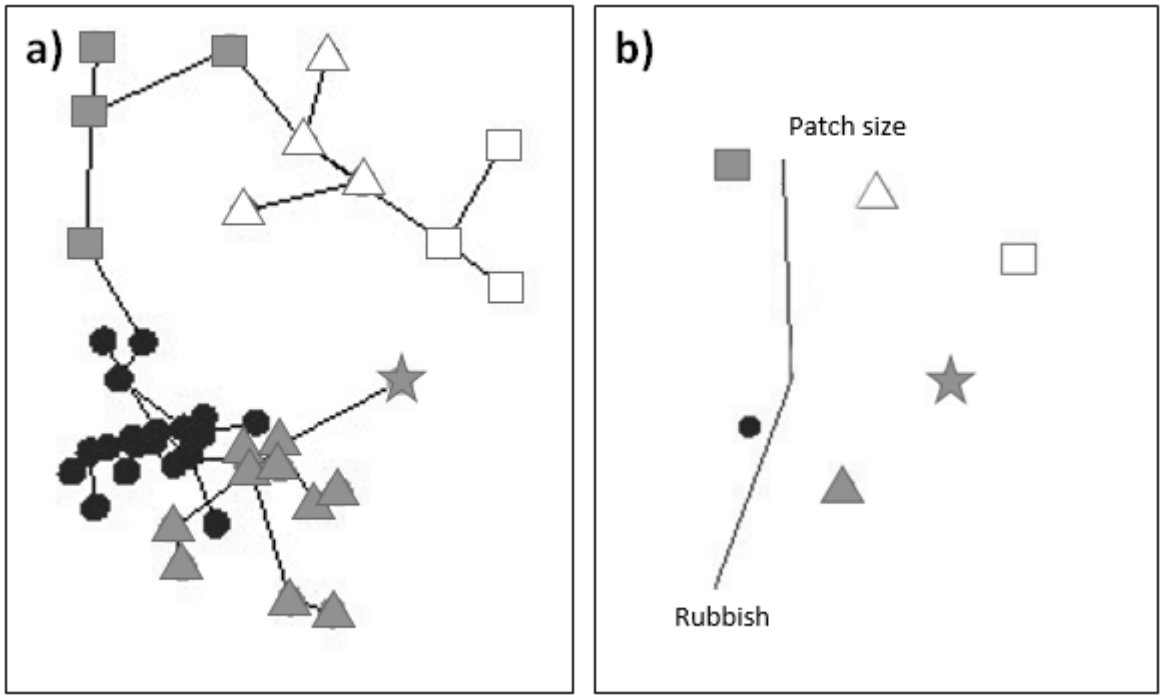


Figure 3.5: a) Two-dimensional ordination (SSH MDS, Stress = 0.1596, Cut-off value: 0.6, 1000 random starts) of 41 patches of remnant urban bushland, based on 24 surrounding land-use variables. Groupings derived through cluster analysis (Fig. 3.4) are also shown. b) Centroids with Monte-Carlos Attributes in Ordination extrinsic variables rubbish and patch size statistically significantly correlated with ordination axes.

Six groups emerged in cluster analysis based on surrounding land use (Figure 3.4). Groups one and three are characterised by patches that were previously surrounded by remnant vegetation in 1965 that has since been cleared. Group two had higher proportion of parklands as surrounding land-use in 1965 than groups one and three. Groups four, five and six represent patches in long established areas, that is, much of the remnant vegetation was cleared prior to 1965. Group four had a higher proportion of parklands in 2015 than five and six, whereas group six had a higher proportion of parklands in 1965 than groups four and five.

3.6.2 Disturbance variables affect patch size and nemesiids

There was only one significant result when using patch as a unit of measurement. Thus, rubbish intensity was negatively correlated with patch size ($p = 0.029$, F stat: 5.126). Using quadrats as a unit of measurement, there was a highly significant negative correlation between rubbish and patch size ($p < 0.0001$) (Table 3.2). However, rubbish had no significant impact on mygalomorph presence or absence (Table 3.2).

Table 3.2: ANOVA output from StatistXL Microsoft Excel plugin package. Analysis at quadrat level to determine any significant relationships between disturbance variables (Grass, rabbits and litter) and whether this correlates presences/absences of nemesiids (PR_AB) with patch remnant vegetation (PRV) as a covariate in urban extent of Swan Coastal Plain, Western Australia. * indicates significant p-values.

Y Variable	Source	Type III SS	df	Mean Sq.	F	Prob.
RABBIT	PRV	1.782	1	1.782	27.692	0.000*
	PR_AB	0.641	2	0.321	4.982	0.008*
GRASS	PRV	0.011	1	0.011	0.100	0.752
	PR_AB	1.323	2	0.661	5.794	0.004*
RUBBISH	PRV	1.469	1	1.469	51.402	0.000*
	PR_AB	0.051	2	0.026	0.894	0.411

The presence of rabbits was found to be negatively correlated with presence of mygalomorphs ($p = 0.008$) and positively correlated with size of patch ($p < 0.001$). Invasive grass was significantly negatively correlated with nemesiid presence ($p = 0.004$) but was not significantly correlated with patch size (Table 3.2).

3.7 Discussion

Urbanisation is a relatively recent process in the region with Perth being established in 1829, but with rapid and extensive clearing after the 1950s (Figure 3.2). Long-term effects of clearing, changing land-use, disturbances and conservation practises may not yet be apparent due to the relatively short time frame. However, attempting to identify threatening processes at early stages is imperative for effective conservation management, especially in terms of mitigating cost both to the environment and to the economy.

3.7.1 Change of surrounding land-use affect disturbance and nemesiids

Correlation between size of patch and surrounding land use groups is reflective of recent developments in urban planning, as smaller patches are more common in more recently established areas. Commonly, patches of remnant vegetation are adjacent to or surrounded by parkland. Rubbish was also more common in more recently established areas. Rubbish penetrates smaller patches more readily in a form of edge effect. Since rubbish was not found to influence nemesiid presence, this was an inconsequential finding for this study but was included as potentially important in future studies.

Surrounding land-use may be a major driver of disturbance factors. One of the initial reasons change in land-use was incorporated in this study was the speculated high mobility of male mygalomorphs. There have been many incidences where males were collected that had been caught walking against fences and walls, presumably attempting to traverse between patches. If reproductive rates were subsequently reduced due to higher male mortalities since 1965, then ghost populations could have occurred. Although ghost populations were not found in this study, the effects of change in surrounding land use are an important parameter to be incorporated in future studies of mobility relating to threatening processes. This may be especially important for species with medium to high dispersal and/or mobility capabilities that are long-lived, for example Red-tailed (*Calyptorhynchus banksii*) and Carnaby's Cockatoos (*Calyptorhynchus latirostris*) (Saunders 1990; Joseph, Emison, and Bren 1991) or pollinators (Kremen *et al.* 2007). For more mobile species, visitation or nesting could be mapped within or between patches then compared to cluster analysis of change in land-use variables, for example comparing Figure 3.2 with Figure 3.4 and 3.5. We suggest that distribution mapping, in conjunction with cluster analysis, be implemented in future studies to assess if change of land-use impacts on long lived species.

3.7.2 Disturbance variables affect patch size and nemesiid presence

Disturbance of habitat due to invasive species (rabbits and invasive grass) has a significant impact on nemesiid species. However, patch size does correlate with some disturbance variables (rubbish and rabbits, but not invasive grass) with greater impact being seen in smaller patches than larger patches. Greater disturbance in smaller patches has been noted in other studies in Perth remnants (Stenhouse 2004) and may be attributed to edge effect (Saunders, Hobbs, and Margules 1991). Nevertheless, the direct impact of these phenomena on arthropods remains unclear (Bolger *et al.* 2000). Intuitively any impact would be applicable to other mygalomorphs in the Perth metropolitan area.

Invasive grass may be more concerning as a threatening process for all mygalomorph species as it considerably alters ground-level strata. It may seem that high degree of invasive grass may obscure visibility of burrows. However, those that were persisting in areas of high weed invasion tended to be highly visible as they were exhibiting mounding behaviour; a bare, raised area mound of sand that surrounded approximately 20 cm around the burrow entrance. It was concluded that visibility was not compromised and is not considered a limitation.

Invasive grass would impact not only on the foraging behaviour of other mygalomorph species, but the presence of invertebrate species that serve as prey. Invasive grass is cause for concern for not only the choking effect it may have on mygalomorphs and native vegetation (Stenhouse 2004; Mason, Bateman, and Wardell-Johnson 2018) but also adding to fuel loads during summer die-off and increasing the likelihood of damaging fire (Anderson 1982; Rossiter *et al.* 2003). Invasive weed management through regular herbicide regimes and community involvement is highly recommended.

Rabbit diggings potentially disturb mygalomorph burrows to the point that they are no longer found in rabbit-occupied areas. During the survey, the entrances of many non-nemesiid burrows were pulled from the ground by rabbit diggings. Though it was primarily rabbits that seemed to be disturbing mygalomorph burrows, this form of disturbance was also occurring where bandicoots had been re-introduced (Figure 3.2, #34). Mygalomorphs may be experiencing less disturbance from digging presently (in areas where rabbits are not present) than in the past. Prior to European settlement in 1829, bandicoots and other small mammals were prevalent throughout the region. Therefore, in areas without rabbits, mygalomorphs may be experiencing fewer disturbances from digging than in the past. This lack of disturbance may explain the especially high density of mygalomorphs in some areas with low rabbit presence. Alternatively, a higher abundance of prey species benefiting from human influence in these patches may allow greater numbers of mygalomorph spiders to be supported, as has been seen in golden-orb spiders (Lowe, Wilder, and Hochuli 2014). Mitigating the intensity of rabbits through practises such as fumigation of active warrens is recommended to all organisations in Perth that assist in management of remnant bushland.

Rubbish was not an effective variable to gauge human disturbance, as rubbish was accumulating around the edges of patches, paths and fencing. Quadrat results were more predictive of presence and absence than patch data for disturbance variables. Unsurprisingly, this means patches are not exhibiting uniform processes and should not be analysed as such. Patch is likely at too large a scale and may present false negatives (Type 2 error) when analysed.

3.7.3 Mobility and dispersal capabilities affects conservation

Fahrig (2013) proposed the habitat quantity hypothesis; to challenge the use of habitat patches as natural units of measurement. In support, using quadrats as a unit of measurement was far more insightful into the effects of disturbances; likely due to the low dispersal and mobility of the species.

Fragmentation and isolation may have varied effects with species mobility capabilities (Thomas 2000).

Traditionally, criteria for conservation priorities are based primarily on distribution range. As Runge (2014, 2015) suggests this may be detrimental to mobile species that may be experiencing threatening processes that occur over a large scale. Arguably, protection of ranges could be applicable for some endangered species that receive extensive funding for protection. For most cases though, this is not an economic use of resources to protect most species (Harvey *et al.* 2011). Categorising conservation status based on mobility and dispersion of species and associated threats may be a more effective approach, as has been recently done with 'nomadic' species (Runge *et al.* 2015). Mobility capabilities would also be useful for distinguishing between local and landscape effects, as they would have varying impacts (Melles, Glenn, and Martin 2003).

Considering the impact of invasive species demonstrated in this study, threatening processes should be further prioritised in management in SWA. Harvey *et al.* (2007) also concluded that small patches should be conserved for non-passerine bird species and reptiles in Perth, a conclusion likely related to dispersion and mobility capabilities. In the case of mygalomorph spiders, phenology varies between clades (Ferretti *et al.* 2012). Life history events in SWA seem to be triggered by seasonal events of high humidity, perhaps relating to their vulnerability to desiccation (Mason *et al.* 2013).

Significant gradients of rainfall, temperature and vegetation types occur along in SWA hotspot (Sander and Wardell-Johnson 2011). In mygalomorphs, this may allow for greater genetic diversity through both adaptive variation and natural divergence caused by isolation (Moritz 2002; Main 2003). Exceptionally high biodiversity and endemism in SWA are explained by climate stability, landscape age and fire predictability (Mucina and Wardell-Johnson 2011). In conjunction, poor dispersal and poor mobility capabilities, while speculative, may contribute to speciation (Harvey *et al.* 2011), especially in-situ speciation (Rix *et al.* 2014).

3.7.4 Conservation management implications

Habitat clearance is the first and foremost threat to mygalomorphs as they will not be able to readily disperse back into rehabilitated areas from adjoining uncleared land (Yen 1995). There has been no record of nemesiid burrows occurring outside uncleared remnant vegetation. Continued habitat clearance occurs at an alarming rate in urban areas of Perth due to urban sprawl. The Perth

urban area has more than doubled since the 1970s due to large-scale land clearing (WWF-Australia 2010). Thus 6 812 ha of natural bush, (average 851.5 ha per year) was cleared in the Perth metropolitan area from 2001-2009, (WA Local Government Association's Perth Biodiversity Project). To put this sprawl into perspective, Perth population density (310 people /km^2, is 0.05% that of London (5490 /km^2) and 0.03% that of New York City (10756 /km^2). Urban sprawl is not only a foremost cost to natural environments, but is also a major economic concern as low density living makes public services less effective and more expensive (Nechyba and Walsh 2004).

Clearing is especially problematic for smaller patches, being allocated less value despite being able to retain high biodiversity over time (Stenhouse 2004; Guénard, Cardinal-De Casas, and Dunn 2014). This study has demonstrated the value of small patches for nemesiids, and most likely other mygalomorphs, with viable populations being confirmed from a 10 000 m^2 quadrat, within a 2.7 ha patch (#4, Figure 3.1). It should also be noted that due to landscape effects there may be some species that remain only in small, isolated patches. As many species are yet to be discovered, described and requirements understood (Yen 1995; Harvey *et al.* 1997), the clearance of even small, isolated patches could potentially destroy the last remaining population of a species. The high biodiversity consequences of deforestation in this global biodiversity hotspot suggests a need for a ban on further clearing of remnant vegetation within the Perth Metropolitan Area. This would need to be enforced by the EPA and would have wide significance for urban planning in the region.

The current guidelines for short-range endemic sampling (EPA 2009) make it very difficult for status and associated protection for potential species to be assigned. It has been established that there are clades with low dispersal, fecundity and mobility capabilities and that this makes them more vulnerable. It would be appropriate to protect immediately rather than wait for distribution maps of species with low taxonomic resolution. Considering the impact of threatening processes outlined in this study, an IUCN red-list conservation status of (at least) 'vulnerable' for all mygalomorph species, and other clades considered potential SREs, occurring in Perth is recommended.

3.8 Conclusions

Very low dispersal and mobility capabilities seem to allow for ongoing persistence in high quality urban remnant native vegetation patches for mygalomorphs over time. However, management practices to limit the impact caused by rabbits and invasive grass should be prioritised in future management. Protection of clades that exhibit any short-range endemism traits should be

implemented immediately and enforcement of no further clearing of remnant bushland in this biodiversity hotspot. We predict that if high quality habitats are maintained, there will be ongoing persistence of mygalomorph populations, even in small patches. If management suggestions are adhered to, there seems no reason mygalomorphs, and other species with poor mobility and dispersal, could not persist indefinitely within urban remnants.

Chapter 4

The pitfalls of short-range endemism: high vulnerability to ecological and landscape traps

"Mankind is the only kind of varmint sets his own trap, baits it, then steps in it"

~ John Steinbeck (1902 – 1968)

4 The pitfalls of short-range endemism: high vulnerability to ecological and landscape traps

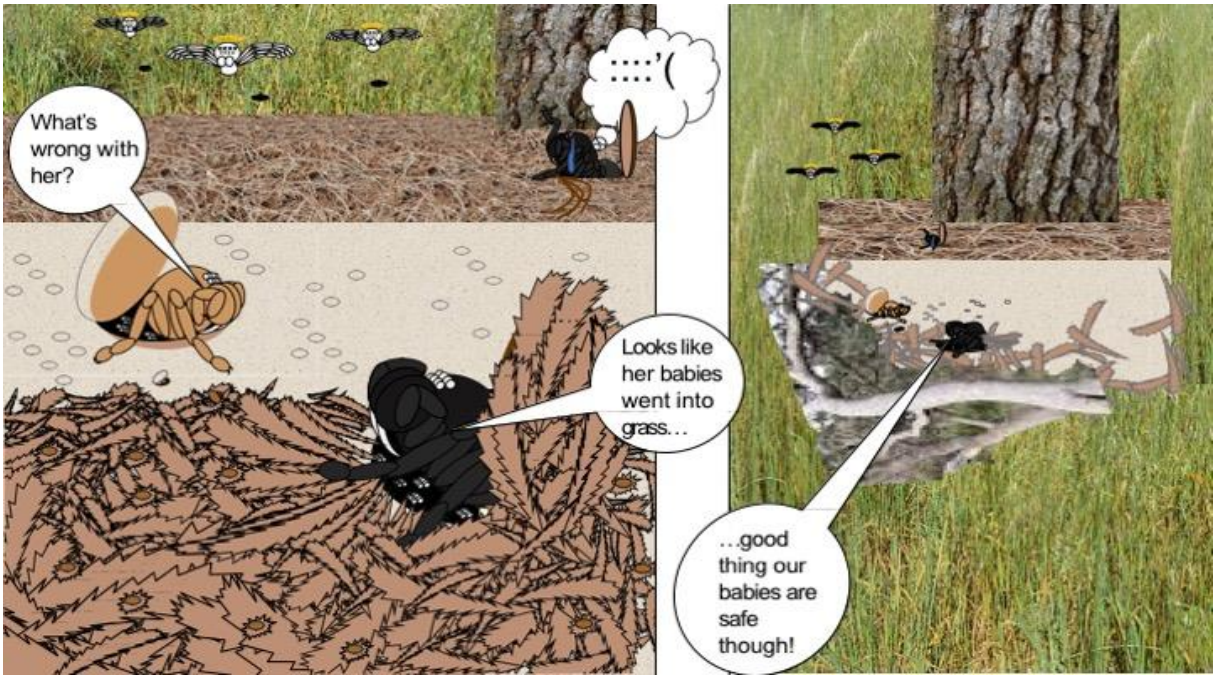
4.1 Impact Statement

Grass lures one species

For others grass destroys niche

Danger for groovers

4.2 Graphical abstract



4.3 Abstract

Ecological traps attract biota to low-quality habitats. Landscape traps are zones caught in a vortex of spiralling degradation. Here, we demonstrate how short-range endemic traits may make such taxa vulnerable to ecological and landscape traps. Three short-range endemic species of mygalomorph spider were used in this study: *Idiommata blackwalli, Idiosoma sigillatum* and an undescribed *Aganippe sp*. Mygalomorphs can be long-lived (> 43 years) and select sites for permanent burrows in their early dispersal phase. Spiderlings from two species, *I. blackwalli* (n=20) and *Aganippe sp.* (n=50), demonstrated choice for microhabitats under experimental conditions, that correspond to where adults typically occur *in situ*. An invasive veldt grass microhabitat was selected almost exclusively by spiderlings of *I. sigillatum*. At present, habitat dominated by veldt grass in Perth, Western Australia, has lower prey diversity and abundance than undisturbed habitats and therefore may act as an ecological trap for this species. Furthermore, as a homogenising force, veldt grass can spread to form a landscape trap in naturally heterogeneous ecosystems. Selection of specialised microhabitats of short-range endemics may explain high extinction rates in old, stable landscapes undergoing (human-induced) rapid change.

4.4 Introduction

Habitat-selection theory suggests behavioural and life history decisions prompted by environmental cues act as indicators of habitats that maximise fitness (Rosenzweig 1981). Misguided habitat choice may be based on environmental cues associated with high-quality habitats but that are no longer reliable in disturbed or changing environments. Choices based on such cues lead to organisms entering 'ecological traps' (Dwernychuk and Boag 1972; Delibes, Gaona, and Ferreras 2001). Ecological traps pose a serious conservation concern for a wide range of taxa (Battin 2004; Hale, Treml, and Swearer 2015; Hale and Swearer 2016). A review of ecological traps shows that historically, most studies have focused on highly mobile bird species and their choice of nesting sites but more recently there has been attention to other, commercially relevant, taxa (Robertson, Rehage, and Sih 2013). Here we argue that ecological traps are particularly threatening for short-range endemic (SRE) taxa. Persistence of these taxa is further compromised in disturbed landscapes for two main reasons 1) their specialist co-evolutionary requirements, and 2) limitations in their capacity to relocate following disturbance.

Highly disturbed landscapes form 'landscape traps', compromising ecological function and compounding the influence of ecological traps for many taxa (Lindenmayer *et al.* 2011). For example, logging and altered fire regimes can interact in ways that cause the irreversible modification of ecological function. Landscape traps may also be associated with negative feedback loops between fire and weed invasion (Fisher *et al.* 2009). Thus, fire provides opportunity for weed invasion, which then provides greater fuel loads, increasing the capacity for more intense fires.

Regions with high proportions of endemic taxa represent a unique and ongoing challenge in conservation biology worldwide (Wardell-Johnson and Horwitz 1996). Landscape age may explain high endemism and biodiversity in some sites (Mucina and Wardell-Johnson 2011) with complex microhabitats and niche partitioning having established and evolved over time in stable conditions (Rosenzweig 1981). Old, stable landscapes may therefore be more susceptible to landscape traps due to increased numbers of associations – providing a higher chance of disturbances that lead to negative feedback loops (Lindenmayer *et al.* 2011). Historical divergence in old, stable landscapes may be primarily attributed to two major factors 1) heterogeneously distributed habitat and narrow, subdued geographical barriers (Wardell-Johnson and Horwitz 1996), and 2) taxa with limited mobility and dispersal capabilities (Rix *et al.* 2014).

A taxon with a distribution of less than 10 000 km^2; low reproductive output and limited mobility and dispersal are criteria for SRE taxa (Harvey 2002). SREs are of high conservation concern as a restricted distribution contributes to rarity and increased chance of extinction (Harvey 2002). Vulnerability is exacerbated when combined with a limited capacity to adapt or escape human-induced rapid environmental change (HIREC) (Sih, Ferrari, and Harris 2011). SREs tend to be specialists, and representation is proportionally higher in invertebrates than vertebrates (Harvey 2002). Old, stable landscapes are likely to have the highest numbers and proportions of SREs globally (Rix *et al.* 2014).

The ancient and highly heterogeneous landscape of south-western Australia (SWA) hosts many SRE species (Rix *et al.* 2016). By their nature, SREs are typically rare and cryptic, making it difficult to gather essential information for conservation decisions. Poor dispersal capabilities suggest that SREs can survive in small patches of high-quality remnant vegetation (Mason, Wardell-Johnson, and Main 2016). Mygalomorph spiders are excellent candidate taxa as bioindicators for SRE taxa. They are sedentary, meaning individuals can be monitored long-term. Choice of microhabitat by a dispersing spiderling is a vital first step to successful investment in a life-long burrow. Burrows

are investments in terms of effort and time to establish. It is rare for mygalomorphs to move as adults, as such moves come at high energy cost and leave them vulnerable to predation and desiccation (Mason *et al.* 2013). As mygalomorph matriarchs can live up to 43 years (Mason, Wardell-Johnson, and Main 2018), appropriate burrow-site and habitat choice by spiderlings is vital.

We aimed to determine whether mygalomorph spiderlings of three species display choice of microhabitat conditions that reflects their realised niche as adults. Realised niche was recorded as adult burrow microhabitats that were regularly recorded during an extensive survey. Burrow microhabitats of adults of each species were used to inform the microhabitat habitat preference choices provided to all spiderling species. Mason *et al.* (2016) suggested that invasive veldt grass (*Erharta* spp.) may be detrimental to local mygalomorph species, either through preventing establishment of burrows, or through microhabitat or prey availability variables. Veldt grass was therefore made available as one of four ground cover choices for mygalomorph spiderlings in a controlled field trial. Microhabitat variables of relative humidity (RH), ambient temperature (Ta) and prey species assemblages (PSA) were also measured to explain spiderling choice.

4.5 Methods

4.5.1 Study site

This study was conducted in Perth, a highly urbanised centre in the Mediterranean-climate zone (mean annual rainfall 740 mm) of SWA. This highly biodiverse region has lost almost 90% of the original habitat due to extensive deforestation and on-going disturbance, qualifying it as a global biodiversity hotspot (Myers *et al.* 2000; Wardell-Johnson *et al.* 2016).

4.5.2 Study species

We collected an individual *Idiommata blackwalli* (Barychelidae - brush-footed trapdoor spiders, body length: 32 mm) with a brood size of 42 and individuals of two genera of Idiopodae (armoured trapdoor spiders); an *Aganippe* sp. (body length: 27 mm) and an *Idiosoma sigillatum* (body length: 36 mm) which had broods of 65 and 78, respectively. The idiopid spiderlings were approximately 3 mm in length and those of *I. blackwalli* 7 mm long. Spiderlings stay within their mothers' burrow until they are ready to disperse. All spiderlings used in this study were found hatched within the burrow and collected with the mother. To accommodate the mother and her brood until they were ready to naturally disperse, I used glass jars filled with soil from the corresponding site of

collection. As burrow shafts were destroyed during collection, cardboard tubes were used to provide a hollowed area, otherwise surrounded by the soil in the jar. A stocking sock was used to transport mothers and spiderlings into the cardboard tube, so that the length of the sock may allow them to move up and down the shaft of the tube. The top of the sock was tied off well above the soil level so that I could easily determine when the spiderlings may be ready to naturally leave the burrow to disperse, as they aggregated at the top. When they were ready to disperse, they were used in the microhabitat choice experiment.

Despite large superficial differences between *Aganippe* and *Idiosoma,* genetic techniques have recently found these genera to be closely related. The extreme sclerotisation of the abdomens of *I. sigillatum* likely relates to behaviour where they block their burrow against intruders. Burrow morphology supports this behaviour by having a diagnostic 'atrium' where the spider can manoeuvre near their lid burrow during foraging, but tightly constricts down the shaft. Foraging range is thought to be enhanced for *I.sigillatum* due to their burrows having twig-line attachments; this enables them to detect prey species along the twigs via vibrations. Both *Aganippe* and *Idiosoma* are highly defensive of their burrows, retreating to the bottom and rearing when disturbed. Conversely, the *I.blackwalli* collected was quite docile by comparison and easily observable in her shallow (15 cm deep) bulb-shaped burrow. Photos of each spider species and their typical burrow entrance has been provided for comparison (Figure 4.1).

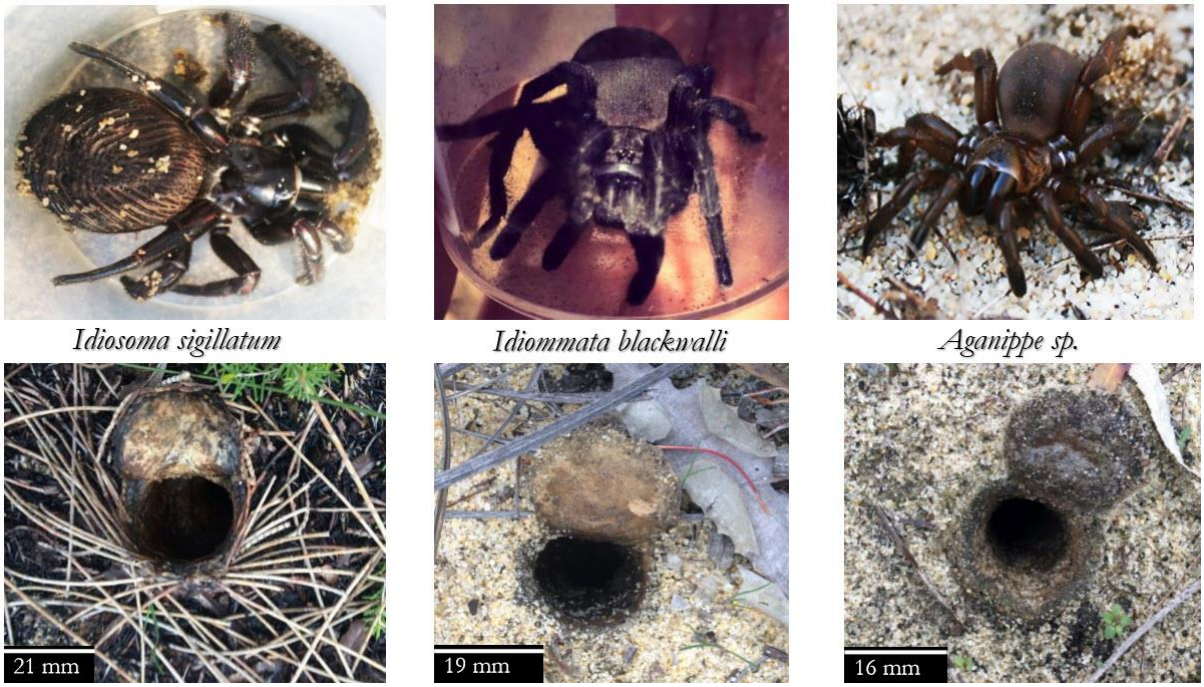


Figure 4.1: Three species of mygalomorph spider used in the study and their corresponding burrows. Scale bars in the bottom left corner of burrow photos refers to the widest point across the burrow entrance. All three species occur within patches of urban bushland within Perth, Western Australia. Photo credits: Bill Bateman for *Aganippe* sp. spider, Jessica Moran for *Idiommata blackwalli* spider and Leanda Mason for all others.

4.5.3 Microhabitat preference

Adult spider burrows were located during an extensive survey of Perth urban remnant vegetation that included 135 quadrats (100 m x 100 m) in 41 sites (see Mason *et al.* 2016 for further details). Microhabitat variables to included leaf litter cover (%) and leaf litter type within a one metre square quadrat centred on burrows.

To reflect the natural dispersal time of mygalomorph species a habitat preference experiment was conducted, using the collected spiderlings, from 24th April to 24th May in the field trials area at Curtin University (Bentley campus). Fifty circular enclosures 10 cm high and 30 cm in diameter were constructed from clear plastic, sunk three centimetres into the sand and sealed with cling-wrap to deter spiderling escape (Figure 4.2). Four microhabitat treatments were provided within these enclosures; bare soil, veldt grass tufts, *Allocasuarina fraseriana* (Casuarinaceae) and *Banksia attenuata* (Proteaceae) litter (Figure 4.2). Within each enclosure, configuration of microhabitats was divided into eighths with the two replicate treatments positioned directly opposite one another (Figure 2). An individual spiderling was released in the centre of each enclosure and the location of their burrow recorded on the following day. The position of the spiderling was also recorded an hour after release to see if they had moved. Chi-square tests were performed for each species

using StatistXL v.1.9 to identify microhabitat preference, both in adults and by dispersing spiderlings.

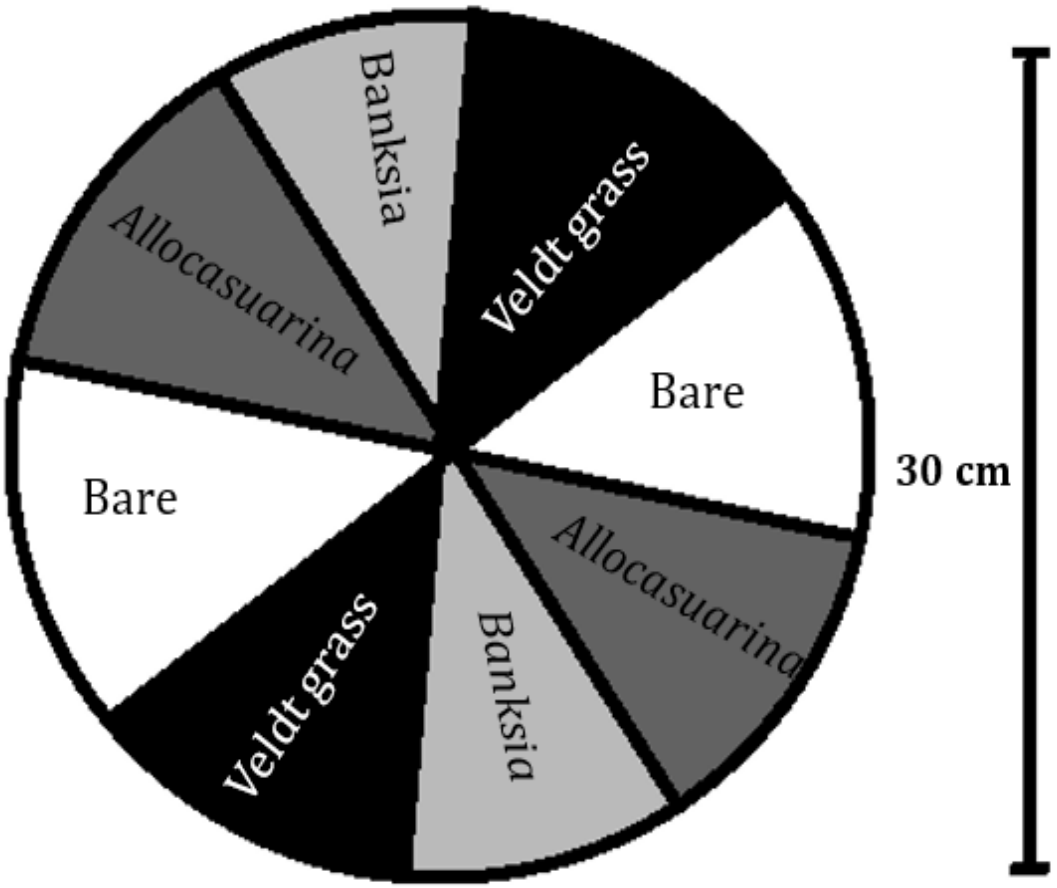


Figure 4.2: Design of spiderling enclosures used in this experiment in south-western Australia. Spiderling microhabitat enclosures diameters were 30 cm wide with 10 cm tall clear plastic walls, sunken 3 cm into sandy soils. Four treatment types were available for mygalomorph spiderlings to select for a burrow location; bare ground, veldt grass tufts, *Allocasuarina fraseriana* and *Banksia attenuata* leaf litter. All experiments were conducted at Curtin University Bentley Campus (Perth, Western Australia) during April and May 2016.

4.5.4 Microhabitat characteristics

Ambient temperature (Ta) and relative humidity (RH) was recorded hourly using iButtons in each of the four microhabitat types in the field; bare ground, veldt grass tufts, leaf litter of *A. fraseriana* and leaf litter of *B. attenuata*. Ten iButtons were placed in each microhabitat type at two remnant bushland study sites (Kings Park: 31°57'46.0"S 115 °49'52.8"E and Bold Park: 31°56'53.1"S 115°46'13.6"E) and at the spiderling experiment field trial area (32°00'43.1"S 115°53'23.1"E). All iButtons were placed where leaf litter and top layer of soil interacted, except for bare soil microhabitats where iButtons were placed on top of the soil. Records of Ta and RH during 24th May to 6th June 2016 were used for analysis.

To assess abundance and diversity of potential prey species, we collected twenty *in situ* ground-cover samples for each of the four microhabitats; ten from Bold Park and ten from Kings Park. Samples were collected within a 20 cm x 20 cm quadrat and were pooled from the same microhabitat and site. Samples were placed in a light-funnel for a week and leaf-litter invertebrates were collected in a jar filled with 100 mL of ethylene-glycol. These invertebrates were later categorised by size and recognisable taxonomic units (RTUs) (Oliver and Beattie 1993).

4.6 Results

4.6.1 Microhabitat preference

Significant differences in microhabitat preference were found for all three species. Adult microhabitat corresponded with spiderling microhabitat preferences for both *Aganippe* sp. and *I. blackwalli*; spiderlings of these two species preferred open ground cover and *B. attenuata* leaf litter, respectively (Table 4.1).

Table 4.1: Microhabitat preferences for three mygalomorph spider species (*Aganippe* sp., *Idiommata blackwalli* and *Idiosoma sigillatum*) spiderling establishment under controlled experimental conditions in Perth, south-western Australia. The number of adult burrows found in situ ground cover microhabitats (*Allocasuarina, Banksia*, bare ground, veldt grass) is shown.

	Species	*Allocasuarina*	*Banksia*	Bare ground	Veldt grass	n	d.f.	p value
Spiderlings	*Aganippe sp.*	8	12	21	9	50	3	0.04
	Idiommata blackwalli	3	11	3	3	20	3	0.01
	Idiosoma sigillatum	2	0	0	38	40	3	< 0.001
Adults	*Aganippe sp.*	1	2	10	0	13	3	< 0.001
	Idiommata blackwalli	3	15	0	0	18	3	< 0.001
	Idiosoma sigillatum	17	4	4	0	25	3	< 0.001

Idiosoma sigillatum, a species that typically attaches twig-lines to the rim of their burrow, were predominately found in *A. fraseriana* leaf litter as adults, but selected veldt grass almost exclusively as spiderlings (Table 4.1). In these cases, no twig-lining was apparent, with one exception where *Allocasuarina* litter from an adjacent treatment was used. All spiderlings were recorded to have moved from the centre of the enclosure after one hour, though none had yet established a burrow, some were (11 spiderlings) recorded as being in the same treatment area.

4.6.2 Microhabitat characteristics

A comparison between microhabitat Ta revealed little difference, with all averaging between 14°C and 15°C. Variability in Ta remained most stable in *B. attenuata* leaf litter (range: 23.0, SD: 3.9), followed by veldt grass (range: 23.2, SD: 4.2), *A. fraseriana* leaf litter (range: 23.3, SD: 4.5) and bare ground (range: 26.0, SD: 5.3) (Figure 4.3).

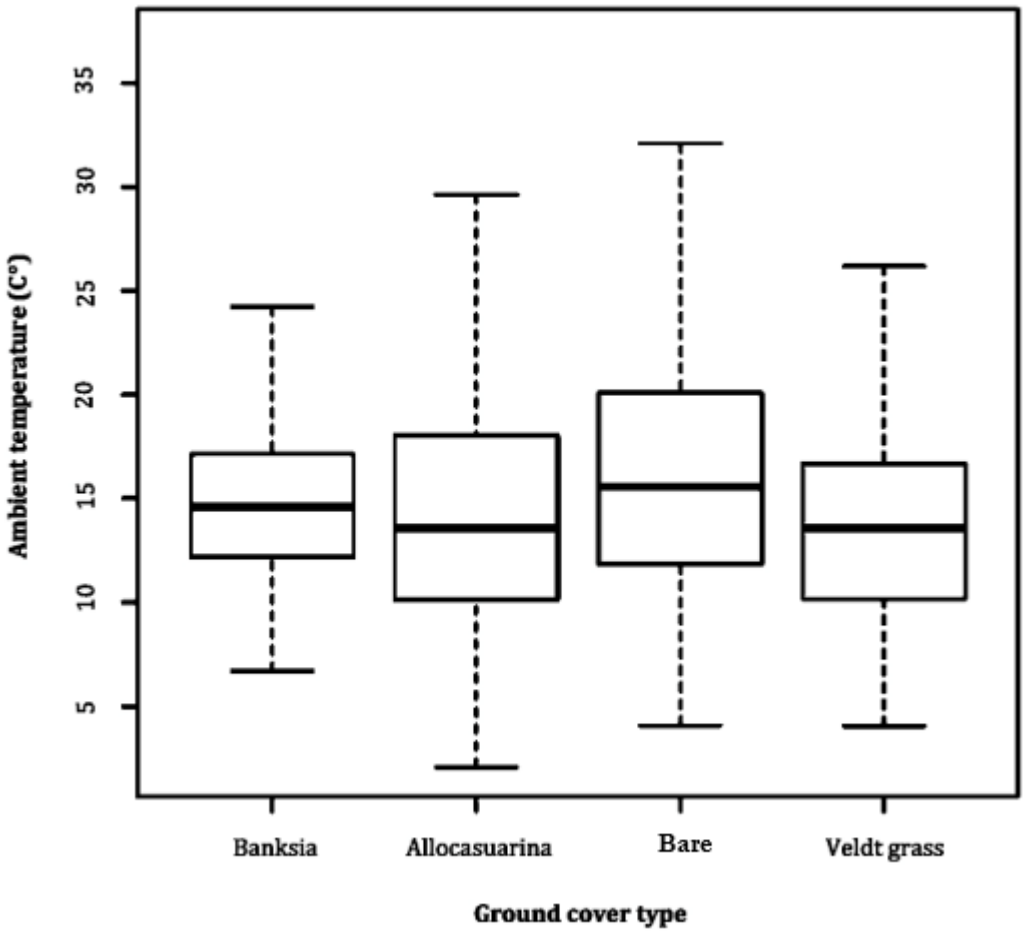


Figure 4.3: A box-and-whisker plot comparing the differences in ambient temperature (C°) fluctuation during 24th May – 6th June, 2016 in different ground cover types (*Banksia* leaf and *Allocasuarina* leaf litter, bare ground and veldt grass) found in urban bushland of Perth, Western Australia.

Relative humidity exposed far greater difference between microhabitats. Leaf litter of *B. attenuata*, leaf litter of *A. fraseriana* and open ground cover all averaged 87.2 - 87.4%. However, a higher RH (93%) was found in veldt grass. Veldt grass retained the most moisture (range: 51.7, SD: 10.5), followed by leaf litter of *B. attenuata* (range: 62.9, SD: 12.6), leaf litter of *A. fraseriana* (range: 43.8, SD: 10.6) and open ground (range: 72.2, SD: 15.5) (Figure 4.4).

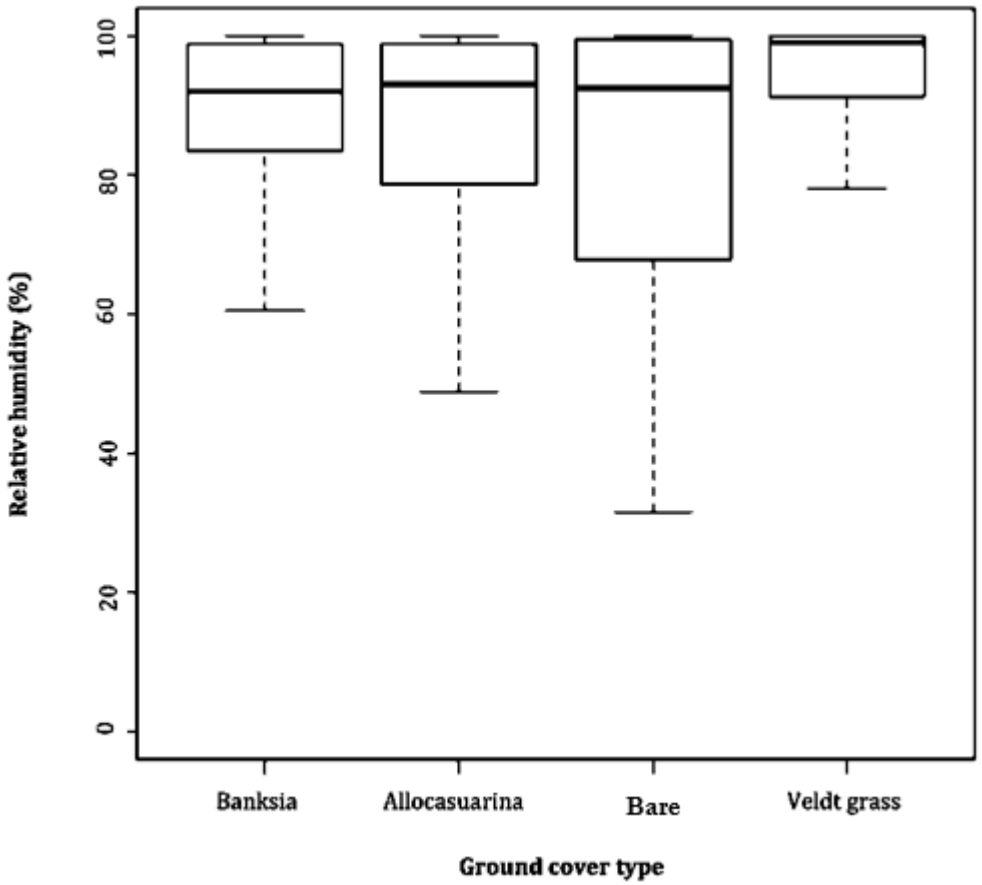


Figure 4.4: A box-and-whisker plot comparing the differences in relative humidity (%) fluctuation during 24th May – 6th June, 2016 in different ground cover types (*Banksia* leaf and *Allocasuarina* leaf litter, bare ground and veldt grass) found in urban bushland of Perth, Western Australia.

The size of potential prey species varied greatly between microhabitat types. Size classes of 0.5 - 1 mm and 9 - 10 mm yielded high numbers (i.e. n < 100) across all microhabitats and can be attributed primarily to two RTUs being Collembola (springtails). Veldt grass yielded the least potential prey in both abundance and species richness (n: 213, S: 10). By comparison, open ground had greater numbers (n: 483) but similar species richness (S: 11) while *Banksia* leaf litter provided more species (S: 21), but lower abundance (n: 393) than open ground. The most productive ground cover was *A. fraseriana* with both highest abundance (n: 6591) and richness (S: 23) (Table 4.2).

Table 4.2: Number (n) of Recognisable Taxonomic Units (RTUs) per size class (mm) for each microhabitat type (Bare, Veldt grass, *Allocasuarina* and *Banksia*). Twenty in situ ground-cover samples for each of the four microhabitats; ten from Bold Park and ten from Kings Park in Perth, Western Australia. Samples were collected within a 20 cm x 20 cm quadrat and were pooled from the same microhabitat and site.

	Bare		Veldt grass		*Allocasuarina*		*Banksia*	
Size (mm)	n	RTUs	n	RTUs	n	RTUs	n	RTUs
0 - 0.5	0	0	3	1	15	1	18	1
0.5 - 1	69	2	108	1	6099	3	144	2
1 - 2	351	6	9	2	84	8	66	6
2 - 3	0	0	3	1	45	1	36	2
3 - 4	3	1	3	1	12	2	18	2
4 - 5	9	1	3	1	3	1	6	2
5 - 6	0	0	0	0	21	1	0	1
6 - 7	0	0	0	0	3	1	0	0
7 - 8	0	0	0	0	36	1	0	1
8 - 9	0	0	0	0	3	1	0	0
9 - 10	51	1	57	2	255	2	66	2
10 - 11	0	0	0	0	0	0	33	0
11 - 12	0	0	0	0	6	1	3	1
12 - 20	0	0	3	0	0	0	0	0
20 - 30	0	0	0	1	0	0	0	1
30 - 40	0	0	24	1	9	1	3	1
Total	483	11	213	10	6591	23	393	21

4.7 Discussion

Habitat choices consistent with an ecological trap were revealed by *I. sigillatum* spiderlings, as they showed a high preference for invasive veldt grass over native *A. fraseriana* leaf litter (where adults were typically found). *Idiosoma sigillatum* spiderlings appeared to have fallen into an ecological trap, as indicated by five factors. Firstly, a high RH in veldt grass may have enticed the spiderlings into this microhabitat. High RH may be an evolutionary trap for this species, as high RH is a physiological requirement for mygalomorphs (Mason *et al.* 2013). Secondly, *I. sigillatum* is one of a few mygalomorph species in SWA that have a "moustache" twig-line arrangement attached to their burrow rim. This is apparent even as spiderlings when establishing in *A. fraseriana* leaf litter. Foraging capabilities may therefore be further compromised when establishing in veldt grass. Thirdly, previous studies have indicated that veldt grass compromises ecosystem functioning (Fisher *et al.* 2006) and this appears to be supported by our data on low prey species abundance and diversity in veldt grass in comparison to *A. fraseriana*. Fourthly, if, in the wild, *I. sigillatum* spiderlings disperse into veldt grass patches, then there is no evidence they have persisted to adults.

Lastly, should spiderlings initially establish in veldt grass and later move, this would result in high energy costs, and leave them vulnerable to predation and desiccation.

Mygalomorph spiders have exceptionally low fecundity, rendering the probability of locating a brooding mygalomorph spider mother during single surveys very low (Main 1978). Therefore, we were exceptionally fortunate to conduct this study using three individual broods from three species. While there is potential for maternal effects on habitat preference, life history and realised niches of mygalomorph adults suggest a low likelihood of a change in outcome. Our confirmation of mygalomorph spiderling choice in microhabitats is novel. We therefore suggest investigation in other mygalomorph spiders with ready access to brood, such as tarantulas that are routinely used in the pet trade.

The impact of invasive grasses effectively transforms and homogenises the ecosystem. By facilitating and interacting with other transforming processes (e.g. nutrient status and fire regime) these grasses form a landscape trap (Fisher, Loneragan, Dixon, and Veneklaas 2009). Reliance on microhabitats, as demonstrated by *Aganippe sp.* and *I. blackwalli*, and other SRE species (Harvey *et al.* 2011), means that the spread of veldt grass to form a landscape trap is likely to be a threatening process (Figure 4.5).

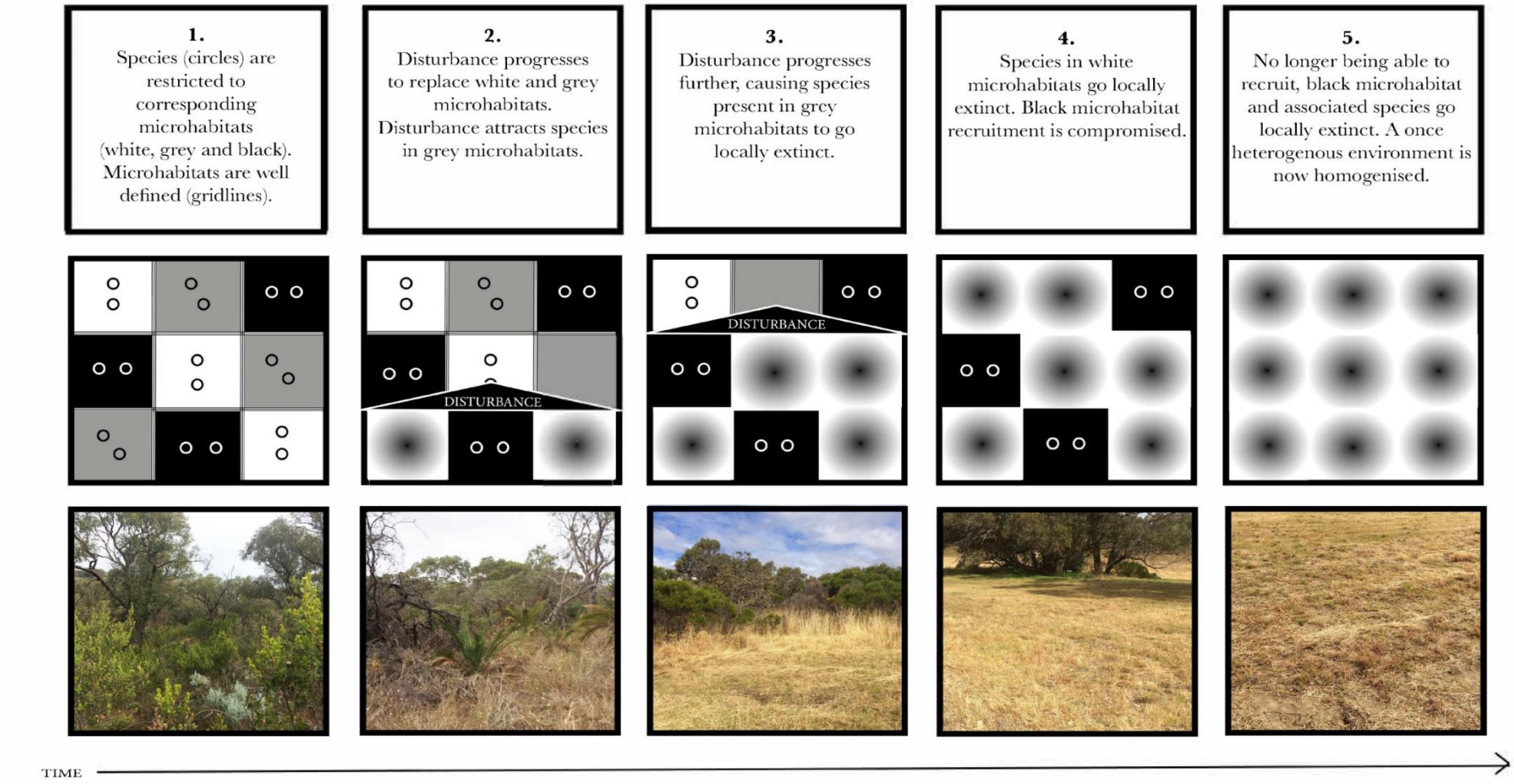


Figure 4.5: Hypothetical representation of short-range endemic species in response to ecological traps and landscape traps over time. The example, including all photographs, is from Bold Park in Perth metropolitan area of Western Australia. Photo credit: Leanda Denise Mason

As an invasive weed, veldt grass tends to homogenise environments by out-competing native species (Fisher *et al.* 2009) and replacing microhabitats. In highly heterogeneous environments that harbour a high diversity of specialist, endemic and co-evolved taxa, homogenisation poses a significant threat to biodiversity (Wardell-Johnson and Horwitz 1996). Homogenisation of previously heterogeneous habitats is the underlying cause for biodiversity loss worldwide. This has significance for the transformation of native habitats through human land-use practices (Sih, Ferrari, and Harris 2011). In terms of effective management, re-introduction of native species into habitats after a homogenising disturbance would be a poor use of resources (Fisher *et al.* 2009). Preventative rather than restorative measures is required (Wardell-Johnson *et al.* 2016). Restoration is impracticable for the level and time required to rebuild complexity and associated microhabitats (Rebelo *et al.* 2011). The prevention of likely ecological traps and determination of the circumstances that transform them into landscape traps is imperative for conservation decision-making.

Sedentary taxa enable reliable monitoring of individuals and populations, generating invaluable data for conservation decision-making (Main 1978). Most mygalomorph species exhibit the SRE traits of low mobility, low dispersal, low fecundity, slow growth, restriction to microhabitats, and entire distribution being less than 10 000 km^2 (Harvey 2002). Some mygalomorph species have capacity to balloon (Pétillon *et al.* 2012), but this may have evolved to mitigate fatal territorial behaviour (Mason unpublished data) rather than to increase dispersal capability. As such, the biology of SRE groups will still need to be considered in management for conservation. Mygalomorphs provide an excellent exemplar of how other SRE may react to novel threatening processes. Unfortunately, exceptionally long lifespan and low reproductive output mean that reduction in fitness, through habitat clearance, disturbance and degradation e.g. through weed invasions, may already be causing localised extinctions in mygalomorphs and other SREs.

We found invasive veldt grass to be a poor-quality microhabitat compared to native microhabitats due to lower prey species richness and abundances. Veldt grass provides an example of ecological and landscape traps in which SRE taxa, such as mygalomorphs, may be caught. In a global context, all specialist species that cannot readily re-locate or adapt are particularly vulnerable to the formation of landscape traps through homogenisation of native microhabitats. While broad-scale management would be ineffective in heterogeneous environments (Wardell-Johnson and Horwitz 1996), targeting specific, widespread traps, such as weed invasion, may control homogenisation and consequent extinctions.

4.8 Conclusions

Informed justification allows cost-effective investment in conservation decision-making. Human-induced rapid environmental change is a significant threat to biodiversity in old, stable landscapes, which are prevalent globally (Mucina and Wardell-Johnson 2011). Ecosystem functioning will inevitably be compromised and SRE species will go extinct without appropriate conservation management. Identifying potential ecological and landscape traps early will allow us to better manage SREs and other specialist taxa prevalent in heterogeneous habitats. Further studies into the interactions between taxa traits and disturbance will allow more effective management, potentially curtailing impacts of current threatening processes.

Chapter 5

Predator guilds show seasonal predilections for model clay spiders in an urban environment

"As king, you need to understand that balance and respect all the creatures, from the crawling ant to the leaping antelope… When we die, our bodies become the grass, and the antelope eat the grass. And so, we are all connected in the great Circle of Life."

~ Mufasa to his son Simba (The Lion King)

5 Predator guilds show seasonal predilections for model clay spiders in an urban environment

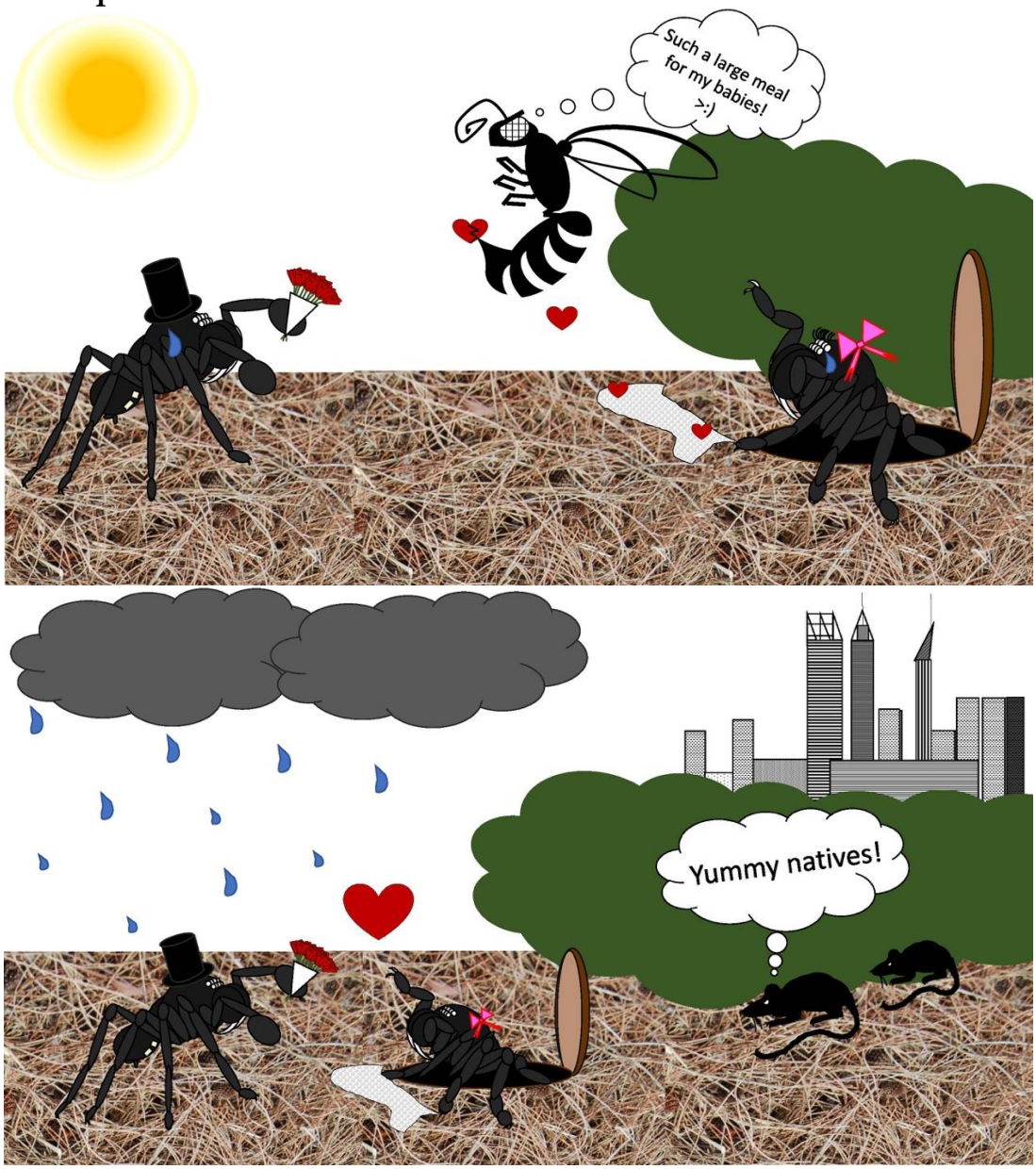
5.1 Impact Statement

Summer hunting wasps

Only attack spiders but the

Invasives more threat

5.2 Graphical abstract



5.3 Abstract

Predator-prey interactions may be altered under human-induced rapid environmental change, such as urbanisation. Extensive clearing in urban areas may leave short-range endemic species, such as mygalomorph spiders, more vulnerable to local extinction through predation in remaining remnants. Predation rates on mygalomorph spiders were assessed using clay models of two size classes (5 cm, 3 cm), during two time periods in 2016 (January – February, July – August). Size and phenology of models resembled the mygalomorph genera *Aname* and *Teyl* occurring in these local urban remnants. Formations of local predator guilds in cluster analysis were significantly influenced by leaf-litter cover (%) and proportion of surrounding parkland. Preference for spider models over control models was consistent across all predation types (bird, rodent, lizard and wasp), but wasps were found to exclusively predate spider models. Generalist predators such as birds, lizards and rodents seem to be opportunistic in comparison to specialist spider wasps (Pompilidae). Lizards and rodents exhibit similar predation behaviour, indicating there may be some inter-specific competition. Invasive generalists (e. g. rodents) or urban adapters (e. g. corvids) are more likely to represent an increased threat to spiders than are co-evolved specialists (e.g. spider wasps).

5.4 Introduction

Since 1960 the global human population has dramatically increased and consolidated in urban centres (Davis 1965; Cohen 2003), contributing to new processes that may threaten fauna (Blair 1996; Fischer *et al.* 2015). Human-induced rapid environmental change (HIREC), such as urban development, can place severe selective pressures on species to adapt to these changes, move away or persist in fragments or refugia within altered landscapes (Sih, Ferrari, and Harris 2011; Sih 2013).

Response to urban environments varies amongst taxa. Although presence of many species is positively correlated with distance from urban environments (McKinney 2008), some taxa, known as 'urban exploiters' e.g. rock pigeons (*Columbia livia*) and some rodents (e.g. *Mus musculus* and *Rattus* spp.) are found mainly in urban landscapes, where they subsist on anthropogenic resources. Other species, e.g. red foxes (*Vulpes vulpes*) globally (Bateman and Fleming 2012) or ravens (*Corvus coronoides*) and butcherbirds (*Cracticus* spp.) (Chace and Walsh 2006) in Australia can be termed 'urban adapters' and benefit from resources such as anthropogenic food or shelter in urban areas but are not limited to urbanised areas. Urban adapters may have profound impact on their native prey species that persist in patches of urban bushland. While urban adapters may thrive in various

landscapes surrounding urban bushland, many native species are restricted to such patches. Negative impacts on native taxa may come from either novel threats (invasive species) or changes in predation behaviour of other native taxa through urbanisation.

Taxa with comparatively low mobility, low-fecundity, poor dispersal and small geographic range traits may persist in very small natural habitat remnants in urban areas if the quality of the patch is maintained (Mason, Wardell-Johnson, and Main 2016), and may be referred to as 'urban engulfed'. These traits are present in many species of millipedes, snails, cicadas and mygalomorph spiders (Main 1987). Such species are known as short-range endemics (SRE) (Harvey 2002) and are of high conservation priority in Australia (EPA 2009; Harvey *et al.* 2011).

SRE species may face extinction as a result of the additional pressure of predation in small, fragmented populations. Differential predation of taxa across urban areas has not been well documented. Research addressing the threat associated with invasive rodents in Australia has often focused on various impacts on native taxa (Burbidge and Manly 2002; Harris 2009; King 1985; Banks and Hughes 2012). There is evidence that invasive rodents can have a severe effect on invertebrates on islands (St Clair 2011), which may be analogous to predation in urban bushland fragments, as many native species may be confined to a single fragment. Reptiles, and lizards in particular, are predators of spiders and other invertebrates (Spiller and Schoener 1990). Reptile response in an urban environment seems to vary markedly between species, with some skinks being urban exploiters or adapters (Prosser, Hudson, and Thompson 2006). Predator-prey interactions involving invertebrates has been poorly represented in the literature compared to vertebrates – probably due to taxonomic impediment and bias towards more charismatic subject species (Harvey *et al.* 2011; Di Marco *et al.* 2017). However, the predation and parasitisation of spiders by wasps (typically members of the family Pompilidae), has been long known (Evans and Matthews 1973). Exploring predator-prey interactions between urban wildlife will assist in understanding complex interactions, and how these may vary under HIREC.

We sought to explore variation of predation on SRE taxa across urban remnant bushland patches. As mygalomorph spiders represent the quintessential SRE taxa, these were selected as subjects on which to base this study. Male mygalomorph spiders reach sexual maturity between 5-7 years, depending on species (Main 1984). Subsequently, males emerge and roam to mate. This venture is a highly seasonal occurrence and appears to vary between species (Figure 5.1).

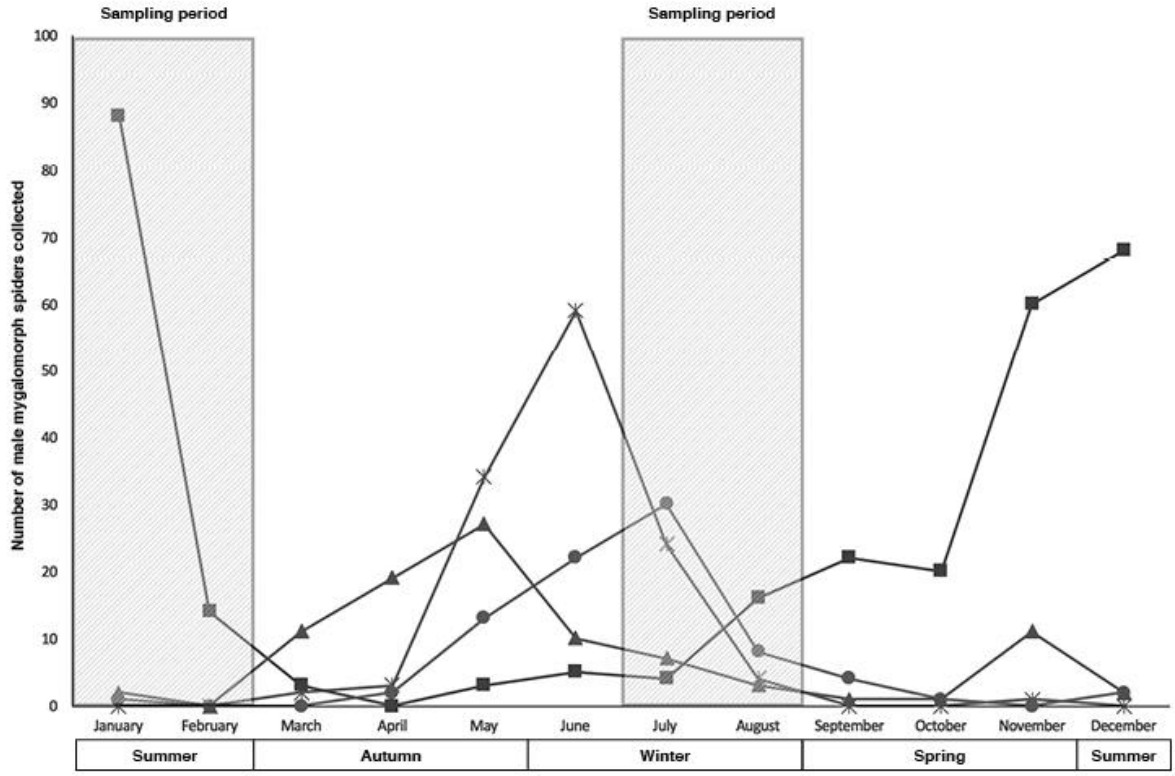


Figure 5.1: Phenology of males of four mygalomorph families (Actinopodidae [×], Barychelidae [▲], Idiopidae [●] and Nemesiidae [■]), collected in Perth, south-western Australia while roaming. Records used from Atlas of Living Australia (ALA) for all years. Grey boxes indicate the sampling period for this study.

For most species in Perth, south-western Australia, male roaming occurs during periods of high humidity in winter, possibly due to physiological constraints (Mason *et al.* 2013). However, one species (Nemesiidae: *Aname mainae),* roams during the summer months. *Aname mainae* is the largest mygalomorph species of the region, reaching up to approximately 5 cm in length. Males of most other species measure up to about 2-3 cm in total body length (Main 1984). These male dispersal events are likely to be the most dangerous times for mygalomorphs as they are exposed to a suite of predators to which they would not be exposed when in burrows. We aimed to test if there were selective or increased seasonal predation of male mygalomorphs while they are exposed on the surface during the mating season. Mygalomorph spider species are known to have specialised microhabitats requirements (Mason, Bateman, and Wardell-Johnson 2018), which means that factors such as leaf litter, mid-storey and canopy cover may vary between species in their exposure to predators. In conjunction with other increased pressures present in an urban context, predation may decrease the chances of ongoing persistence of SREs.

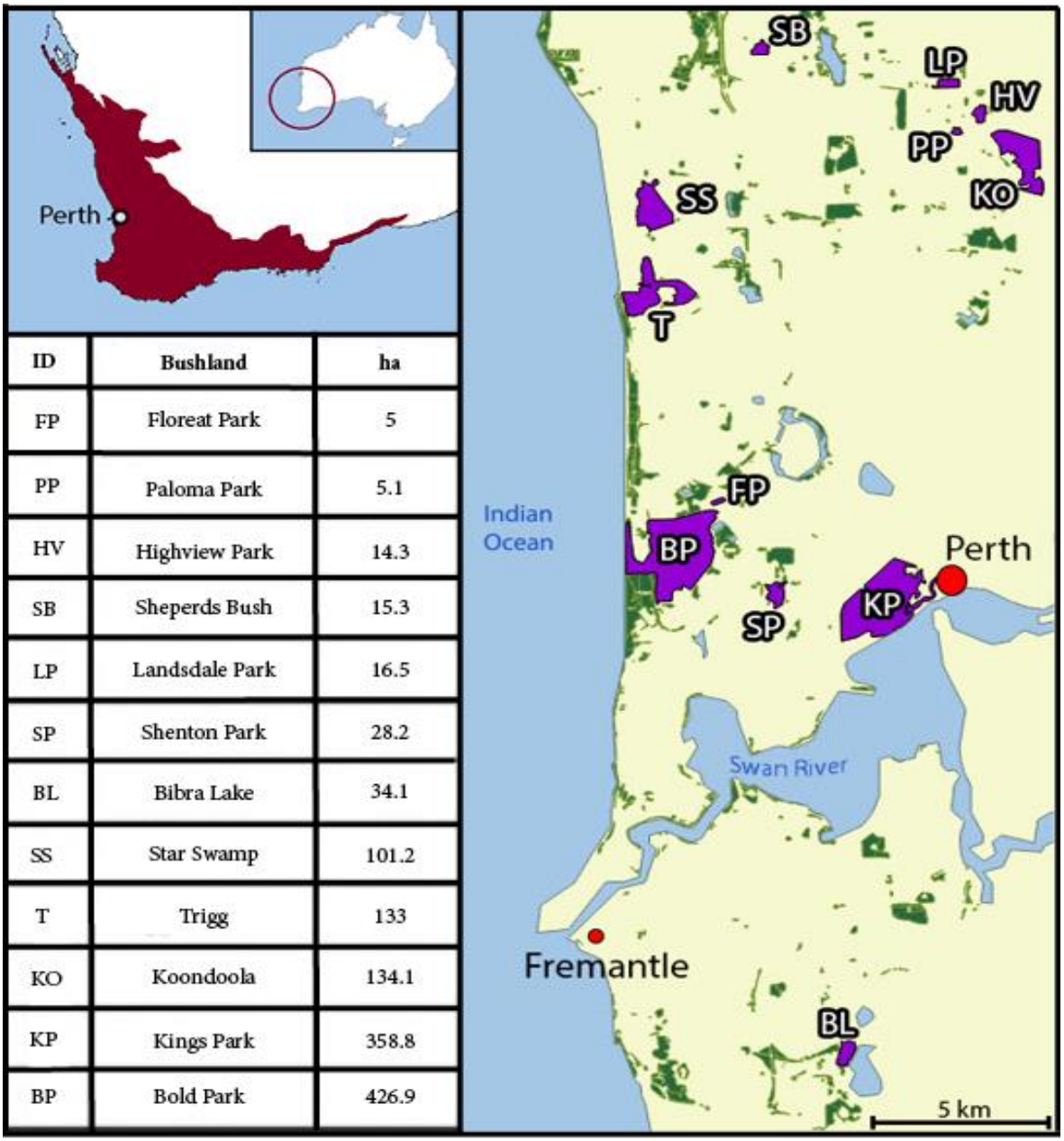
We used clay models to explore the effects of habitat patch size, microhabitat and seasonal predation on spiders in urban areas. Clay models have been successfully used to assess predation on small taxa such as lizards, snakes, mice, invertebrates and bird eggs (Major 1991; Lövei and Ferrante 2017). As SRE endemic taxa are of high conservation priority and predation marks can be confidently identified on clay models, we decided this was the most effective and least harmful approach to test our hypotheses (Lövei and Ferrante 2017). Our study is the first to use clay models to measure predation types, predation size and frequency on mygalomorph spiders. The questions we asked were:

1) What are the local predator guilds?
    a) Is there evidence of competition between identified predator types?
    b) Is surrounding land-use correlated with guilds?
2) Is there a significant difference between predator preferences in terms of spider vs. control, size of model, and season?
3) Is predation frequency by identified predator types influenced by microhabitat variables such as leaf litter, mid-storey and canopy cover?
4) Does identified predator type vary in terms of number of attacks or attack location on the body of the spider?

6.5 Methods

6.5.1 Study sites

All study sites were located within Perth, a highly urbanised centre in the Mediterranean climate (mean annual rainfall 740 mm), South-west Australian (SWA) Global Biodiversity hotspot (Myers *et al.* 2000). Twelve urban remnant sites were selected to provide a range of size categories (Figure 5.2).



ID	Bushland	ha
FP	Floreat Park	5
PP	Paloma Park	5.1
HV	Highview Park	14.3
SB	Sheperds Bush	15.3
LP	Landsdale Park	16.5
SP	Shenton Park	28.2
BL	Bibra Lake	34.1
SS	Star Swamp	101.2
T	Trigg	133
KO	Koondoola	134.1
KP	Kings Park	358.8
BP	Bold Park	426.9

Figure 5.2: Twelve urban remnant bushland sites in Perth urban area used to test predation on clay models. Perth is situated within the biodiversity hotspot of South-Western Australia (SWA). Configured using InDesign with map generated using QGIS Geographic Information System version 2.18.14 (http:/qgis.osgeo.org).

To test any effect of season, sampling was conducted during two different time periods in 2016 (January – February, and July – August). Size and phenology replicate real mygalomorph species that occur in the urban remnant vegetation of Perth (Figure 5.1).

5.5.2 Plasticine models

Predation rates were assessed using 2400 clay models of two size classes (5 cm and 3 cm) (Figure 5.3) and types (spider and control) during two sampling periods. To standardise, spider models

were printed with plastic resin using a 3D printer in conjunction with TinkerCad and UP! Software. This 3D model is available online through TinkerCad as "Spider Model by Leanda Mason". Metal washers of similar size classes were used as controls. Models and washers were uniformly coated with a layer of black plasticine (Flair Leisure Products). Models were connected by transparent fishing wire to a nail pushed into the earth, securing both the model's location and a numbered tag.

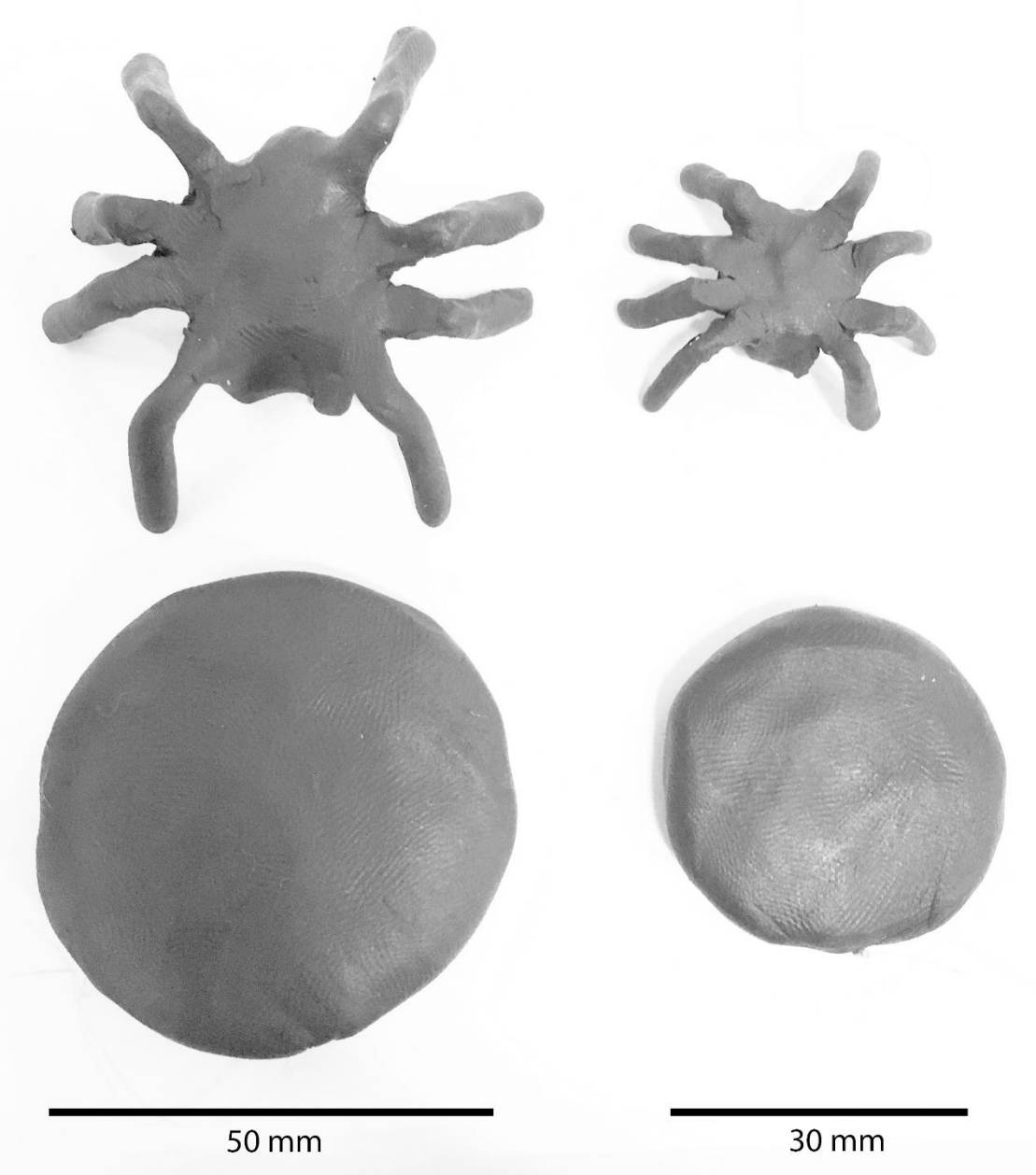


Figure 5.3: 3D printed spider models and washers of two size classes covered in black plasticine clay.

Twenty-five of each of four treatments; small spider, large spider, small control, large control, were placed in a 100 m x 100 m quadrat 10 m apart. Predation type (bird, lizard, rodent and wasp), size

(mm), location on the model and number of attacks were identified from distinctive marks left by predators on the clay models (see Figure 5.4).

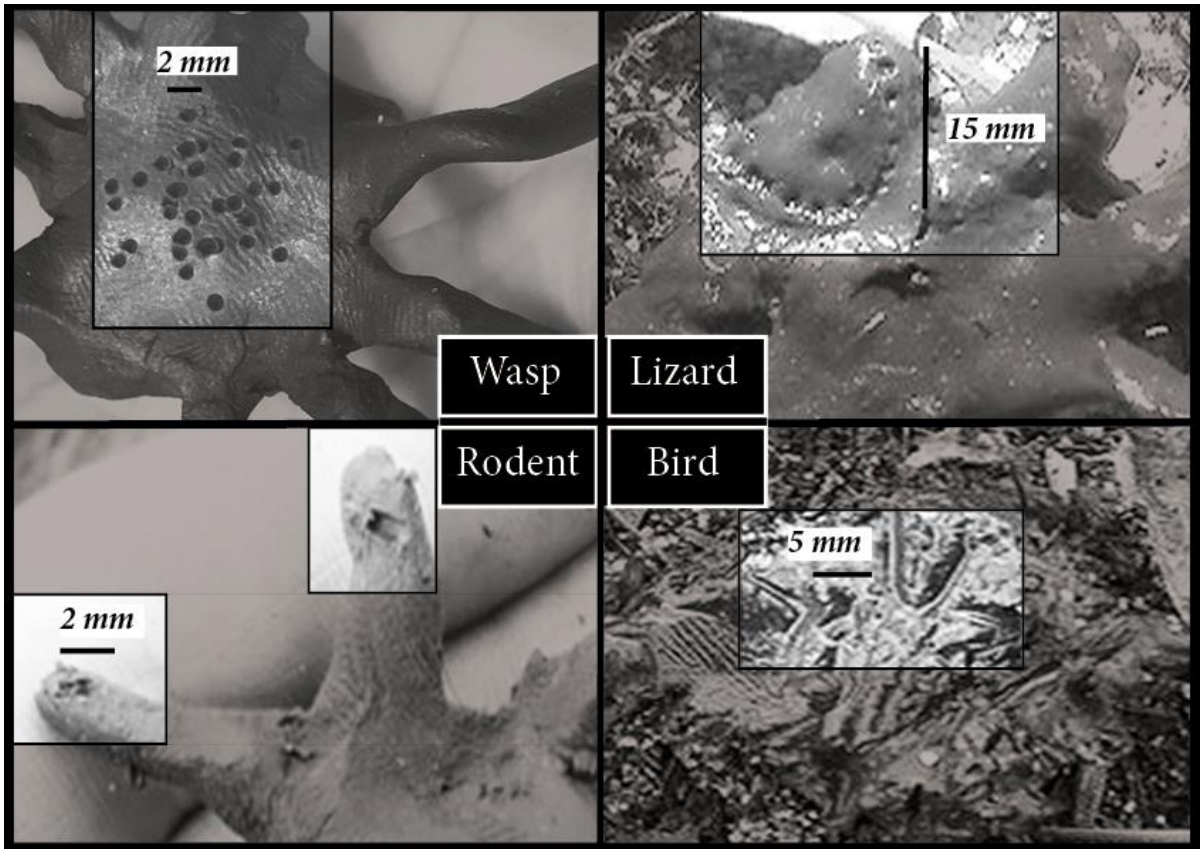


Figure 5.4: Impressions left by predators on clay models in urban remnants in Perth, south-western Australia were identified, measured and location recorded.

5.5.3 Microhabitat and patch variables

Leaf litter type, mid-storey vegetation type and canopy vegetation type were recorded as percentage cover within a 1 x 1 m quadrat surrounding the model, to provide insight into visibility of models available to predators. Surrounding land-use area was measured by generating shapefile layers of buildings, roads, parkland and other remnant vegetation within 250 m, 150 m and 50 m buffers. Buffers were measured for both patch and quadrats in the open source program Quantum Geographic Information System (Team 2017). The Nearmap plugin was used to determine the proportion of different land-use within each buffer area.

5.5.4 Statistical analysis

As this study examines predator behaviour we used predation as intrinsic factors, and determined whether site variables correlated with the resulting multidimensional scaling ordination axes in numerical taxonomic analysis (Calver *et al.* 2010), using PATN3.11 (Belbin 2013). All 2400 models were included in the cluster analysis (predated and non-predated) and converted into a proportion within each unit. Predation types were used as intrinsic factors and combined patch, model type and season were used as separate units (25 models in each unit). The Gower metric was used to determine the degree of similarity between different identified predator types, followed by hierarchical polythetic agglomerative clustering using flexible UPGMA. We used the Two-Step association measure to determine influence of variable groups on identified predator types. A two-way table is a visual representation of the association between different units (guilds) and the influence of identified predator types to form groups. Darker cells show greater association than lighter cells. MDS ordination portrays the spatial relationship between objects in a way that best preserves relative positions. 'Stress' measures the level of distortion from reducing axes (to two in this case), with low stress values (i.e. < o.20) indicating better representation of positions than high stress. The Minimal Spanning Tree (MST) is a form of network analysis that connects each object to its nearest neighbours. If there is a high congruence between cluster analysis, ordination and network analysis, then resulting categories are supported. This allows 'local guilds' (Fauth *et al.* 1996) of predators to be determined and analysis of the influence site variables. Competition within local predator guilds can then also be assessed. During analysis, we found that attack marks from bird species on the clay measuring ≤2 mm and >2 mm birds diverged early. Extrinsic factors were fitted to the ordination using PCC and significance determined using MCAO. The strong clustering formed by using patch, model type and season as units indicated that these factors may having be useful in predicting identified predator type behaviour through multinomial logistic regression.

A MLR was fitted (package nnet, R 3.3.0) using predated data only (n = 510). MLR require a nominal dependant variable with more than two levels and can handle categorical variables (Long and Freese 2001). Model coefficients (logit) represent the change in log-odds of a variables influence relative to the reference category (in this case "birds"). A positive logit indicates the effect of the predictor on predation (relative to birds) is positive. We have used "b" to represent the logit in results. Predator type (bird [145], lizard [139], rodent [150], wasp [76]) was the response and site, site size, season, model size and type, attack number, attack location and litter, understory and canopy cover the predictors. Data were split into a train and test set (80% train, 20% test) and the packages 'caret' and 'e1071' used to assess classification accuracy. The package stargazer (Hlavac 2015) was used to plot significance levels. Predator size categories were reduced for analysis to: 1 (A), 2 (B) and >2 (C). The location of predation was standardised between model type: 'Body' of spider models were subsumed into 'middle', and spider model 'legs' into 'edge'. The number of attacks was categorised into: 1-4 (A), 5-8 (B) and >8 (C). A multinomial logistic regression was preferred over other GLM's as several predictors were categorical and the assumptions of normality and homoscedasticity could not be met. Additionally, as model size and type were recorded at the within plot scale and were to be included in the analysis, data were not averaged to predation rate per plot.

5.6 Results

Of the 2400 models used, 663 (28%) were predated. From marks on the models predators were identified (Low *et al.* 2014) as birds (33%), lizards (25%), rodents (29%) and wasps (13%).

5.6.1 Local predator guilds

Local predator guilds were defined based on similar predation behaviour across ninety-six model-patch-season units. Six distinct groups were recognised (Figure 5.6): group 1 included two 'model-patch-seasons' units and was based on 'large birds'; group 2 included 10 model-patch-seasons and clustered based on 'wasp' predation. Similarly, 'lizards and rodents' predation behaviour formed group 3, and consisted of twelve spider-patch-seasons units. Group 4 included twelve model-patch-seasons and was based on predation by 'lizards and small birds'. Group 5 included fifty-eight model-patch-seasons and was formed through absence of predation. Group 6 included two model-patch-seasons and was formed from high predation of large spider models across 'all identified predator types, except wasps', in Bold Park in both summer and winter.

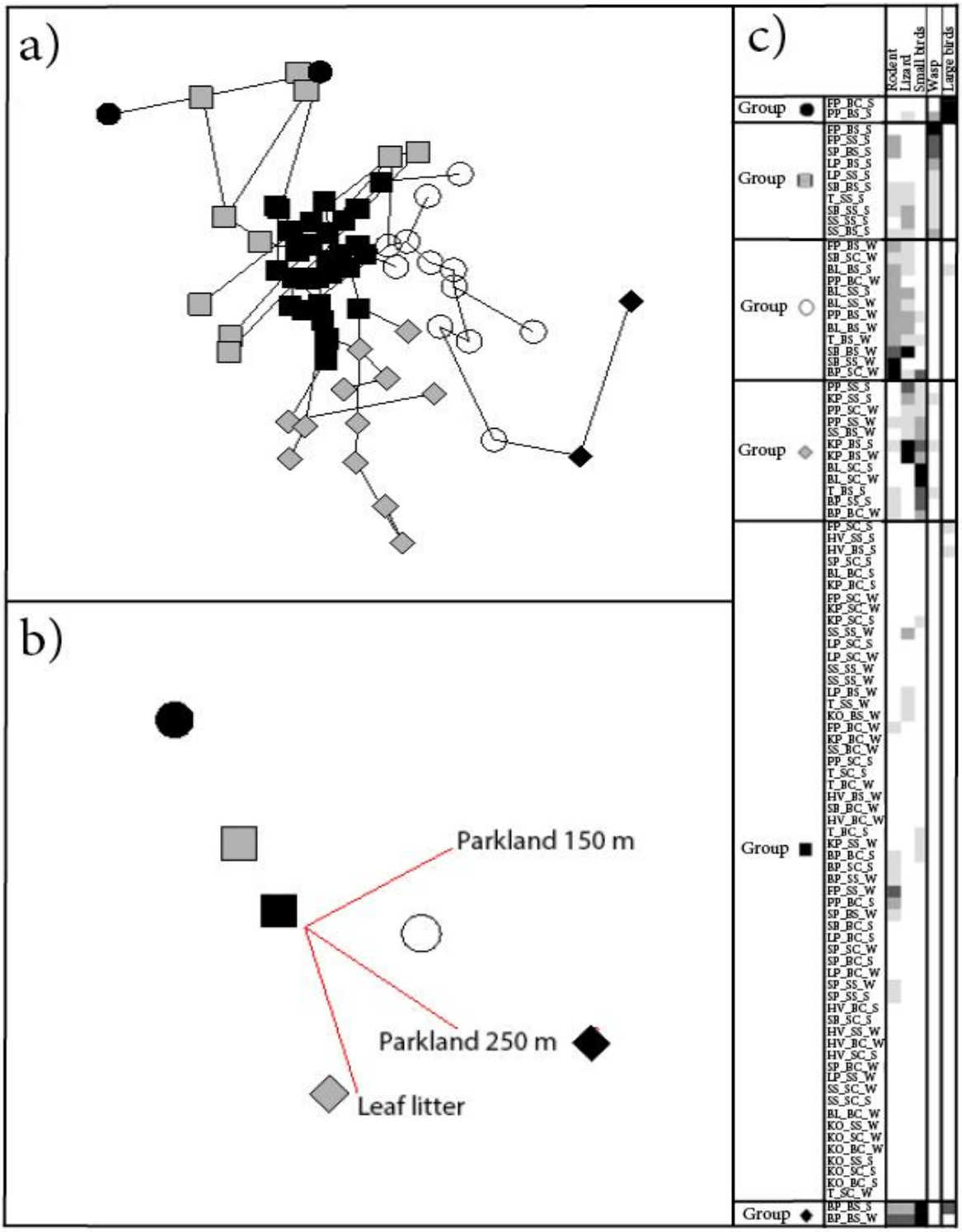


Figure 5.5: 2D semi-strong hybrid (SSH) multidimensional scaling (MDS) ordination (Stress: 0.18) based on ninety-six 'patch-model-season' units and five predation types (Gower Metric Association Measure, Classification Strategy: Agglomerative Hierarchical Fusion, Technique: Flexible UPGMA). Predation types were used as intrinsic factors and combined patch, model type and season were used to separate units. Each "site_model_season" unit presents twenty-five models in the two-way table and are coded as follows: the first line refers to the patch of urban bushland and corresponds to the site map (Figure 4), the second line of codes refers to model type (BS: 5 mm spider, BC: 5 mm control, SS: 3 mm spider and SC: 3 mm control). The third line of code refers to season (S: Summer or W: Winter). a) Significant (MCAO, P < 0.001) extrinsic factors (leaf litter and proportion of surrounding parklands - buffer 150 and 250 m around patches) were fitted using principal PCC. b) Six distinct groups emerged based on predation intrinsic factors. c) Two-way table.

Three extrinsic factors fitted using principal component correlation (PCC) were found to be significant using Monte-Carlo attributes in an ordination (MCAO): leaf litter cover and proportion of parkland surrounding the patch within a 150 m and 250 m zone (Figure 5.5).

5.6.2 Predator predilections

Predator type was modelled using a multinomial logistic regression (MLR). Overall model accuracy was moderate (accuracy 0.70, kappa 0.58, df 72) with significant variables reported in Table 5.1.

Table 5.1: Model type preference (control or spider), size (large or small) and season (winter or summer), and frequency of predation by identified predator type (bird, lizard, rodent or wasp). Multinomial logistic regression was used to determine significance ***: $p < 0.001$, and ****: $p < 0.0001$ within column categories: state, model type and model size.

	Preference		Size		Season	
	Control	Spider	Large	Small	Summer	Winter
Bird	88	128	121	95	84	130
Lizard	34	132	96	70	71	95
Rodent	49	143	113	79	82	110
Wasp	0	89***	55	34	81****	8

Impressions left by wasp predation were found only on spider models. Wasps were the only predator that showed significant ($p < 0.0001$) seasonal differences, predating significantly more in summer than in winter (Table 5.1).

5.6.3 Microhabitat variables

Wasps predated spider models significantly more in areas with lower percentage canopy cover (Table 5.2). Rodents predated spider models significantly more in low percentage understorey canopy cover (Table 5.2). Lizards predated spider models significantly more in areas with high leaf litter and canopy cover (Table 5.2). All birds predated spider models significantly more in low leaf litter and in lower understorey cover areas (Table 5.2).

Table 5.2: Summary of predation type in different microhabitat strata cover (%: leaf litter, understorey and canopy). Values are presented as Mean ± Standard deviation. Multinomial logistic regression was used to determine significance, *: p < 0.05, **: p < 0.01 and ****: p < 0.0001.

	Leaf litter	Understorey	Canopy
Bird	72.7 ± 30.6*	31.8 ± 20.6**	37.7 ± 26
Lizard	77.3 ± 29.7*	32.7 ± 21.8	40.2 ± 27.9**
Rodent	70.5 ± 34.3	28.7 ± 23.2*	34.7 ± 28.2
Wasp	72.8 ± 31.7	38.4 ± 23.5	22.6 ± 25.4****

5.6.4. Predator attack

Majority of models were attacked more (attack number) than once by a single identified predator type but varied significantly among identified predator types (Table 5.3). Birds, lizards and rodents attacked a single model between 1-4 times significantly more than categories with higher attack number. Conversely, wasps attacked models over 8 times significantly more than categories with lower numbers of attack (Table 5.3).

Bird attack rates were similar for both middle and edges of models (Table 5.3). Wasps attacked the middle significantly more than they did the edge of the models (Table 5.3). Lizards and rodents, however, attacked edges significantly more than the middle of models (Table 5.3).

Table 5.3: Location of attacks on models for each identified predation type. Numbers reflect the total number of attacks for each identified predator type within each category. ***: p < 0.001.

	Attack location		Attack number		
	Edge	Middle	1-4	5-8	>8
Bird	61	82	170***	16	4
Lizard	183***	46	135***	12	3
Rodent	192***	59	8	2	66***
Wasp	2	89***	170***	16	4

5.7 Discussion

A clear preference for spider models over controls by all identified predator types indicates that predators were selecting prey based on visual cues, and not only due to curiosity over foreign

objects. The use of controls is surprisingly rare in experiments involving clay models, but is encouraged (Bateman, Fleming, and Wolfe 2017).

5.7.1 Local predator guilds

Predator guilds can have a great impact on prey species (Koss and Snyder 2005) and such guilds may also interact with each other, influencing their impact on prey (Cornell 1993). Prey species that are vulnerable to disturbance (Mason, Wardell-Johnson, and Main 2016) may be further jeopardised by changes in local predator guilds. Disturbance can also change local predator guilds by disrupting available geography and resources that were previously in equilibrium (Cornell 1993; Fauth *et al.* 1996). Generalist predators may be less affected by disturbance than specialist predators as their broad prey niche do not restrict their activities in any particular area (Henle *et al.* 2004). The proportion of land-use surrounding patches constituting parklands was found to significantly influence predator guilds, increasing towards guilds of predominantly rodents and lizards (Figure 5.5: Group O). This may indicate some utilisation of parklands by these predators as an extension outside the patch or avoidance to land-use such as roads buildings.

5.7.2 Predator predilections

In addition to rodent, bird and lizard bite marks - as has previously been recorded in multiple studies using clay models (Bateman, Fleming, and Wolfe 2017) - we also recorded the presence of small piercings on many models (see Figure 5.4) identifiable as sting impressions from spider-hunting wasps. Wasps were found to be the only predator where there was a significantly higher predation rate in summer. Visual recognition of potential prey by wasps in terms of shape (Eberhard 1970) is supported here as wasp predation was exclusive to spider models. Smaller models may be less detectable or may have been preyed upon by different wasp species, indicating a suite of spider-hunting wasp species.

Pompilidae, the family of wasps that prey on spiders, is thought to be highly specific to the species or size of spider prey (Kurczewski and Kiernan 2015), perhaps due to constraints in wasp and/or nest size (Kurczewski and Kiernan 2015). The pompilid *Cryptocheilus bicolor* is commonly seen throughout Australia dragging huntsmen spiders *(*Sparrasidae*)* back to its lair. Records of pompilids collected in Perth (ALA, n = 20) correlate with *Aname* males roaming phenology (October to February), though they also occur through to April. Wasps may not be targeting specific spider species, but a specific size of prey which may depend on size of the wasp (Kurczewski and Kiernan 2015). For example, *C. bicolor* may have been attacking large models

mistaking them for sparrassids of similar size, rather than targeting mygalomorphs. Both *Aname* and some sparrassids, such as *Dingosa* (Framenau and Baehr 2007), have open burrows for which wasps may display similar searching behaviour. However, spider response varies – *Dingosa* avoid wasps by running out of their burrow (pers. obs.), whereas mygalomorphs are more likely to defend burrows through phragmosis i.e. defend the burrow using their body. Predation rates on models are limited in this way as they do not reflect actual outcomes of encounters between wasps and prey.

5.7.3 Microhabitat variables

Microhabitat variables and location of predation events indicate that while rodents and lizards predate at similar rates in the same patches, they occupy different microhabitat niches. Lizards preferred to forage in areas with high leaf litter and canopy cover, while rodents preferred to forage primarily in high understory cover. Location of lizard and rodent bite marks on the edge of control models or on the legs of model spiders probably reflects the approach of these predators at ground-level. Most lizards are active during the day, but rodents are nocturnal. As mygalomorph spiders are thought to roam primarily at night (except for *Missulena* which has bright red jaws), predation by rodents may be relatively common. Although bats are known to predate on spiders (Schulz 2000), their contribution to predation rates is not known and no bat bite impressions were identified in this study. Predators may use senses other than visual cues to locate their prey (Vet and Dicke 1992; Tvardikova and Novotny 2012). We suggest future predation experiments either test these factors or be mindful when interpreting results.

5.7.4 Predator attack

Bird predation varied between large birds and small birds in local predator guilds (Figure 6), but not foraging behaviour (Table 5.1). Large birds (> 2 mm peck marks), perhaps due to high mobility capacity, did not have clear associations with other identified predator types (Figure 6). Bird attack rates suggested significantly higher predation in microhabitats with low leaf litter and understorey cover which may reflect a foraging strategy from an above ground vantage point. Similarly, location of attacks on models was seemingly lacking discrimination in birds when compared to ground-dwelling predators.

5.7.5 Implications

As a novel threat, predation by invasive rodents is of high conservation concern (Harris 2009; St Clair 2011; Banks and Hughes 2012) and would affect all local trapdoor spider species, regardless

of season. Displacement and local extinction of native nocturnal predators (multiple small and medium-sized dasyurid carnivores) since Perth was established makes it impossible to know if predation rates are higher, similar or lower for many species than before urbanisation. It is possible that rodents have a similar deleterious effect in native bushland remnants as they do on islands (St Clair 2011). The adaptation of natural predators such as ravens and magpies in urban areas (Lill and Hales 2015; Daniels and Kirkpatrick 2017) may also have a profound impact on spider populations, but potentially only on spiders active during the day (*Missulena*). High predator mobility, in conjunction with a higher abundance, may be especially detrimental to species restricted to smaller patches (Harvey 2002; Harvey *et al.* 2011). We found no significance difference in predation type or rate with size of patch, which is concerning, as it suggests that populations in smaller patches may be more prone to extinction debt (Haddad *et al.* 2015; Kendal *et al.* 2017).

It is possible that predation rates by different taxa are not indicative of an individual attacking one model. For example, a raven may learn quickly that models are not suitable food sources after the first instance. Conversely, a wasp may not learn and continue to attack multiple models in the same area indefinitely. As wasps are highly mobile, attacks on multiple spider models over one quadrat may indicate low levels of learning, rather than a high density of wasps. Similarly, a slow-moving lizard, such as a bobtail (*Tiliqua rugosa*), may encounter only a few models during the week, whereas a fast-moving territorial lizard, such as a scrubland skink (*Morethia obscura*), may encounter many models and multiple times. Site characteristics such as size and microhabitat variables may be accurate indicators for adequate territory ranges for species. For example, rodents may require a much lower territory range to satisfy their diets than would corvids because of the vast differences in size and in niche breadth. For future studies, it is advisable that predator range, if known, be considered when interpreting results in size and connectivity of patches.

As pompilid wasps are native and have co-evolved with native spider species it is unlikely that the impact of their predation on spiders is unsustainable. Indeed, this may be a positive finding for wasp conservation in that, as natural predators of spiders, wasps are still maintaining adequate numbers for survival in an urban context. Similarly, if parasitic wasps are maintaining adequate numbers then abundance of spider prey species are, at present, likely to be sustainable in order to support wasp populations.

5.8 Conclusions

Birds, lizards and rodents are all generalists and operate on different scales making it difficult to assess their realistic impact on spiders. Pompilid wasps are specialists and, although highly mobile, operate at a similar scale to the spiders they prey on. However, as wasps have co-evolved with spiders, predation from wasps will be limited by spider populations. Invasive generalist species such as rodents or urban adapters such as corvids are more likely to be a threatening shift on spiders than co-evolved specialists. It is recommended that replication of this study is conducted over time and in areas with no invasive species to determine changes in rates or proportion of predation. We conclude that the impact of predation on spiders may not in itself be a threatening process, but rather may exacerbate existing threats such as habitat loss, invasive grass and impacts of fires.

Chapter 6

Ashes to ashes: intense fires extinguish populations of urban short-range endemics

"The spread of civilisation may be likened to a fire; first, a feeble spark, next a flickering flame, then a mighty blaze, ever increasing in speed and power."

~ Nikola Tesla (1856 – 1943)

6 Ashes to ashes: intense fires extinguish populations of urban short-range endemics in the South West Australian Global Biodiversity Hotspot

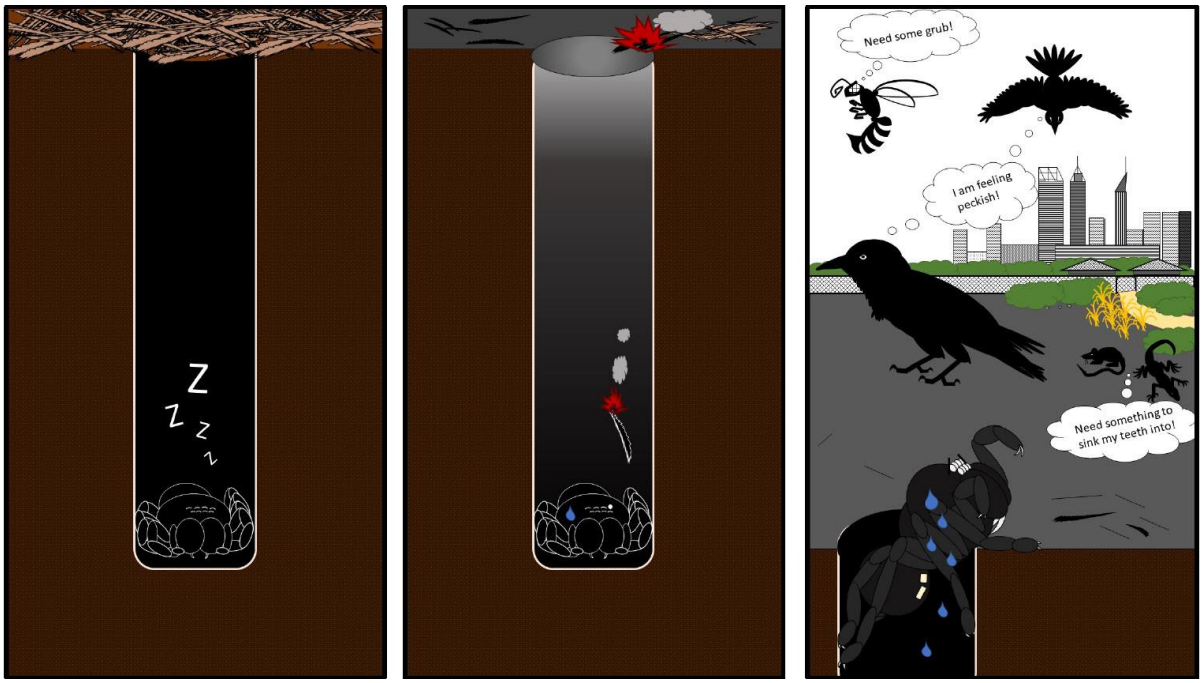
6.1 Impact Statement

Trapdoors survive fire

Aftermath is a threat though

Hunger all around

6.2 Graphical abstract



6.3 Abstract

Native bushland fragmented by urbanisation often experience increased cover of flammable weeds, reduced biomass turnover and an absence of fuel management combined with increased ignitions. Depending on species' mobility and dispersal traits, and the extent of burnt area within remnants, such fires may reduce individual survival rates or limit natural re-colonisation. We monitored initial survival of mygalomorph spiders following two fires in urban remnants of Perth in the South West Australian Global Biodiversity Hotspot. Survival was monitored for a year after both high and low intensity fires. Of 257 burrows found, 115 spiders were initially confirmed to survive after an intense wildfire. None were confirmed alive after 12 months. In sharp contrast, only 1 spider of 103 burrows was confirmed dead after a low intensity prescribed fire. As there were instances of our monitored mygalomorphs relocating a short distance following low intensity fire, we also tested whether predation rates are higher in burnt than unburnt areas. Higher rates of predation were found in burnt areas, but this was strongly influenced by both site and predator type. We recommend further consideration of low intensity prescribed fire, as well as alternative fuel management approaches in urban remnants to better conserve mygalomorph spider populations and other taxa with limited dispersal and/or mobility capabilities.

6.4 Introduction

Human land-use modification can be detrimental to the persistence of native arthropod species (Majer and Beeston 1996; McIntyre 2000). In urban areas, clearing of native habitat (Brooks *et al.* 2002) in conjunction with modification of fire regimes (Keeley, Fotheringham, and Morais 1999; Bowman *et al.* 2011) or fuel loads (Haight *et al.* 2004), are shared impacts of human land-use in urban areas. Individual fire events influence taxa to varying degrees, depending on fire intensity, extent and duration (Bradstock, Williams, and Gill 2012). These factors are determined by fuel load, type and arrangement, soil dryness and weather conditions (Scott and Burgan 2005). As fires can be unpredictable and difficult to control due to temporal and spatial fluctuation in such factors, experiments involving fire are inherently difficult to standardise (Mell *et al.* 2010), particularly in urban fragments.

Quantification of the effects of fire on ecosystems is important task in fire ecology (Certini 2005). Native species in Australia that persist in warm, dry, fire-prone climates are often able to do so through evolution of unique adaptive physiological and/or behavioural traits (Gill 1975; Main 1981; Bradstock, Williams, and Gill 2012). Indeed, intermittent periods of aridification, together

with low extinction rates may account for high levels of biodiversity and endemism in south-western Australia (SWA) due to changing selection pressures and refugial habitats (Mucina and Warell-Johnson 2011, Rix *et al.* 2014). The complexity of interactions and high potential for novel consequences associated with changed fire regimes means that greater understanding of fire ecology is imperative in conservation initiatives in these areas.

Fire causes ongoing changes in soil physical and chemical properties (Certini 2005), which is of particular relevance for organisms that live within the soil profile. Intense, fast moving fires do not transfer heat more than a few centimeters (Certini 2005). Fires ignited by lightning strikes or arson have capacity to burn large areas (< 10,000 km^2) (Turner, Ostendorf, and Lewis 2008) and may be a serious threatening process for some taxa. In urban and peri-urban areas, although fire extent may be limited by fragmentation, fires may burn through entire fragments. In the Perth area, fire frequency is lower in smaller remnants, and in more rural remnants (Ramalho *et al.* 2014). In Mediterranean ecosystems globally, fire frequency peaks at an intermediate density of human population (Syphard *et al.* 2009).

Fire events may be especially detrimental for taxa with limited dispersal and/or low mobility capacity; compromising their ability to initially escape fire and later to re-colonise patches. Many terrestrial arthropod species, and some vertebrates, are considered as short-range endemics (SREs). SREs are defined as having a natural distribution range of less than 10,000 km^2 and are of high conservation concern due to low mobility, poor dispersal abilities, low fecundity and being confined to discontinuous or rare habitats (Harvey 2002; Harvey *et al.* 2011). Short-range endemics may have proportionally higher representation in biodiveristy hotspots (Rix et al. 2015). The impacts of urban predators on SRE species, is likely to be a cryptic threat associated with anthropogenic disturbances (Mason *et al.* 2018).

Those mygalomorphs, commonly known as trapdoor spiders, fit this definition of SREs. Mygalomorphs constitute approximately 13% of known species of spiders (Coddington and Levi 1991), and of the 330 known Australian mygalomorph species, 323 are endemic. Mygalomorph species such as *Idiosoma nigrum* (Ecologia 2009; DSEWPC 2013, Rix *et al.* 2018) or *Bertmainus tingle* (Main 1991, Harvey *et al.* 2015) are, to a degree, protected under State environmental law (EPA 2009). Despite the substantial conservation significance of mygalomorph spiders (Main 2001; Mason, Wardell-Johnson, and Main 2016), little is known about their current distribution, habitat requirements and threats to persistence within patches of remnant vegetation worldwide.

Typical life history traits in mygalomorph spiders are likely contributors to the propensity for short-range endemism in this clade (Rix *et al.* 2017). Spiderlings generally disperse and establish within a relatively short distance – usually less than 500 m (DSEWPC 2013) of their natal burrows (Main 1984). However, in most cases they disperse no further than within the leaf litter of the nearest tree to their natal burrow (Main 1957, 1978, 1982, 1987). After establishment of their first burrow, mygalomorph spiders seldom abandon it naturally (Main 1984). While females can live up to 43 years (Mason, Wardell-Johnson and Main 2018), males perish after reaching sexual maturity at 5 - 7 years (Main 1978, 1984). It is unknown how long mature males may be able to survive above ground, or how far they might be able to travel during their highly species-specific seasonal adventure to find a mate (Mason *et al.* 2018). In an urban context, many unnatural barriers inhibit traversing between isolated or otherwise disjunct bushland patches. Survival of females outside their burrow (in less than 80% relative humidity) for more than 48 hours is unlikely due to desiccation (Gray 1968; Mason *et al.* 2013).

Soil heating during fire decreases rapidly with depth (Whelan 1995) and does not penetrate beyond 20-30 cm depth, regardless of severity or duration (DeBano 2000). However, intense, fast-moving fires do not transfer heat more than a few centimetres in depth (Certini 2005). Prescribed burning is considered an important conservation management tool as it may limit potential impact of intense fire on biodiversity (Fernandes and Botelho 2003; Driscoll *et al.* 2010) through reducing fuel loads. Mygalomorph spiders may be well adapted to survive fires initially (even those of high intensity and long duration) as fire does not penetrate soil deeper (DeBano 2000) than typical depth of burrows. However, fire exposes burrow shafts by burning lids. Secondary effects of fire such as increased opportunistic predation or parasitism, lower prey availability and spider desiccation may impact survival.

We used clay models to explore the effects of predation on spiders in burnt and unburnt treatments of remnant bushland in urban areas. Model sizes mimicked real species of mygalomorph spiders found in our study area; *Aname mainae* (approximately 5 cm) and most other species (2-3 cm) (Mason *et al.* 2018). Controls were used to determine if attacks on models were targeting spiders, or opportunistic (Mason *et al.* 2018).

To explore the impact of burn intensity on the survival of mygalomorphs over time in urban areas we asked the following:

1) Do trapdoor spiders have higher survivability in low intensity fires than in high intensity fires?
2) Are predation rates on spiders significantly higher in burnt than unburnt patches?
3) Does size of spider (using models) increase the rate of predation?

5.5 Methods

5.5.1 Study sites

The study area comprises remnant native vegetation within Perth, a highly urbanised centre in Mediterranean climate (mean annual rainfall 740 mm), SWA. Perth is within one of 35 global biodiversity hotspots (Mittermeier *et al.* 2011), a status declared primarily due to exceptionally high levels of endemism and threat (Wardell-Johnson and Horwitz 1996). Over 70% of native vegetation within the SWA hotspot has been cleared (Wardell-Johnson *et al.* 2016).

At least four families of mygalomorph were recorded; Idiopidae, Barychelidae, Actinopodidae and Nemesiidae but only two species could be confidently identified based on burrow structure alone: *Idiosoma sigillatum* (Idiopidae) and *Idiommata blackwalli* (Barychelidae). In Perth, *Missulena* species of the family Actinopodidae have easily recognisable burrows as all have double-lidded burrow entrances. Nemesiids genuses *Aname, Kwonkan, Teyl,* and *Prochermacha* of Perth and can be distinguished by the complete lack of a burrow lid (Harvey *et al.* 2018).

Here we considered intense fires that fully consumed the entire leaf litter layer at sites. By contrast, low intensity fires tend to retain some burnt leaf litter. Survival of mygalomorphs was monitored after an intense fire in Shenton Park Field Station (Area: 37.0 ha, Co-ordinates: 31°56'59.18"S, 115°48'02.68"E) and after a prescribed, low intensity fire in Kings Park (Area: 358.8 ha, Co-ordinates: 31°57'49.32"S, 115°49'52.93"E). Three sites were then used to measure effect of fire on predation of clay model spiders in unburnt and burnt areas following intense fires in Kensington Bushland (Area: 9.3 ha, Co-ordinates: 31°59'15.97"S, 115°53'12.84"E) and Bibra Lake (Area: 48.6 ha, Co-ordinates: 32°05'16.00"S, 115°49'08.70"E), and following a low intensity prescribed fire at Bold Park (Area: 426.9 ha, Co-ordinates: 31°56'54.06"S, 115°46'19.03"E). A map of these sites was generated using QGIS version 2.18.14 (Figure 6.1) (Team 2017).

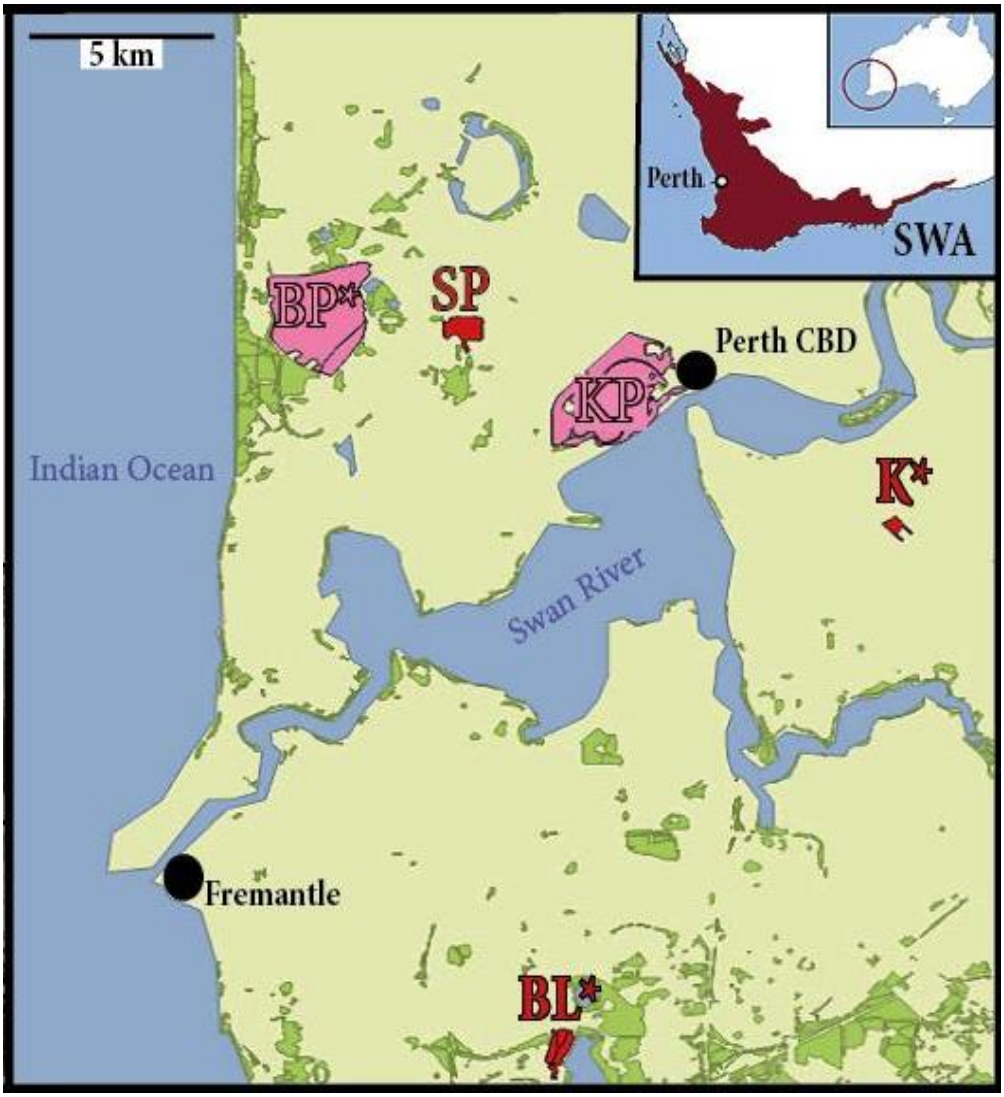


Figure 6.1: Map of low intensity burns (pink), high intensity burns (red) and predation experiments (*) study sites: Kings Park (KP, May 2015), Bold Park (BP, April 2016), Kensington (K, February 2016), Bibra Lake (BL, February 2016) and Shenton Park Field station (SP, January 2014) within Perth, south-west Australia (SWA). This map was generated using QGIS Geographic Information System version 2.18.14 (http:/qgis.osgeo.org).

6.5.2 Burrow Survival

Post-fire surveys were conducted using a targeted survey, using 100 m x 100 m quadrats with 100 m transects spaced 10 m apart. Burrow diameters and GPS location were recorded and a metal peg with flagging tape and a permatag with an ID number attached was placed 20 cm to the north of the burrow. Burrows were visited every month and any changes such as re-lining of silk and construction of lids or invasion by ants or weeds, were recorded.

The Underwood Ave Bushland (Figure 6.1) fire started from a faulty powerline in January 2014. The site was visited every three months for a year. Kings Park and Bold Park (Figure 6.1) were burnt at low intensity, in May 2015 and 2016 respectively, by prescribed burns conducted by the

Botanical Park and Gardens Authority (BPGA). Both Bibra Lake Reserve and Kensington Bushland (Figure 6.1) were burnt during February 2016 through wildfire, the latter a case of arson.

6.5.3 Predation

Predation rates were assessed using clay spider models of two size classes (5 cm and 3 cm) to mimic the range of sizes in trapdoor spider species present in Perth (Mason et al. 2018). For standardisation, spider models were printed with plastic resin using a 3D printer in conjunction with TinkerCad and UP! Software, the blueprint is accessible through TinkerCad as "Spider Model by Leanda Mason". Metal washers of similar size classes were used as controls in order to determine if predation behaviour in post-fire conditions was specific to spiders or not. Models and washers were uniformly coated with a layer of black modelling clay (Flair Leisure Products). Models were connected by transparent fishing wire to a nail pushed into the earth, securing both the model's location and a numbered tag.

It is acknowledged that this experimental layout includes pseudo-replication (i.e. many sample points, but only one site for each treatment). This places limits on the generalisability of our findings. However, comparison of fire effects on predation behaviour was achieved by placing sampling grids in burnt (impact) and unburnt (control) areas at the same site.

Twenty-five of each of four treatments; small spider, large spider, small control, large control, were placed in a 100 m x 100 m quadrat 10 m apart and collected after one week. Due to the design of the experiment, units were separated by location (site), whether they were placed in a burnt or unburnt quadrats (state) and the type of model treatment (model). Using site-state-model units was the lowest possible separation that incorporated all variables that may influence predation. Predator impression type (bird, lizard, rodent and wasp), size (mm), location on the model and number of attacks were identified from distinctive marks left by predators on the clay models. In the case of wasps, attacks on plasticine models would have been an attempt to parasitise spiders by first paralysing and later laying their eggs to consume the spider. For the sake of consistency, if not accuracy, we refer to wasp attacks as predation rather than parasitisation.

6.5.4 Statistical analysis

As some models were unusable for analysis due to melting plasticine or were taken (possibly carried away by birds), data were organised into twenty-four site-state-model units and frequencies converted to proportions for comparison. These twenty-four site-state-model units were also used

to assess the influence of microhabitat variables (% cover of leaf litter, understorey and canopy) on predation using PATN3.11 (Belbin 2013). As this study examines predator behaviour we used predation as intrinsic factors and determined whether site variables correlated with the resulting multidimensional scaling (MDS) ordination axes in numerical taxonomic analysis (Calver *et al.* 2010). The Gower metric was used to determine the degree of similarity between different predator types, followed by hierarchical polythetic agglomerative clustering using flexible UPGMA. We used the Two-Step association measure to determine influence of variable groups on predator types. A two-way table is a visual representation of the association between different variable groups and particular predator-type groups. Darker cells show greater association than lighter cells. MDS ordination portrays the spatial relationship between objects in a way that best preserves relative positions. 'Stress' measures level of distortion from reducing axes (to two in this case), with low stress values (i.e. < 0.20) providing a better representation than high stress. The Minimum Spanning Tree (MST) is a form of network analysis that connects each object to its nearest neighbours. High congruence between cluster analysis, ordination and network analysis, provides support for the resulting analysis.

A multinomial logistic regression was fitted (package nnet, R 3.3.0) using predated data only (n = 426). Predator type (bird [236], lizard [83], rodent [96], wasp [11]) was the response and site, site size, season, model size and type, attack number, attack location, leaf litter cover, understorey cover and canopy cover as the predictors. Data were split into a train and test set (80% train, 20% test) and the packages 'caret' and 'e1071' used to assess classification accuracy. The package Stargazer (Hlavac 2015) was used to plot significance levels. Predator size categories were reduced for analysis to: 1 (A), 2 (B) and >2 (C). The location of predation was standardised between model type: 'Body' of spider models were subsumed into 'middle', and spider model 'legs' into 'edge'. The number of attacks was categorised into: 1-4 (A), 5-8 (B) and >8 (C). A multinomial logistic regression was preferred over other GLM's as several predictors were categorical and the assumptions of normality and homoscedasticity could not be met. Additionally, as model size and type were recorded at the within plot scale and were to be included in the analysis, data were not averaged to predation rate per plot.

6.6 Results

6.6.1 Burrow survival

Survival was confirmed for 115 spiders of the 257 burrows found after an intense wildfire at Underwood Ave Bushland, but none were confirmed alive after 12 months. All spiders that did

not re-locate after the low-intensity fires, except for one juvenile that died during the fire, survived after 12 months. At least four families of mygalomorph were present; Idiopidae, Barychelidae, Actinopodidae and Nemesiidae but only two species could be confidently identified: *Idiosoma sigillatum* and *Idiomata blackwalli*.

The managed fire at Kings Park was less intense, smaller in extent and of shorter duration than the Underwood Ave fire. Much of the canopy cover remained intact but canopy scorch was evident in some areas. Although the leaf litter layer was burnt during the fire, leaf litter was replaced by dying canopy. Of the 103 burrows found, only one spider was confirmed dead after 12 months – an immature *I. sigillatum* that was burnt during the fire.

6.6.2 Predation

Of the 1091 models used in statistical analysis, 426 were predated (39%). Predation included 236 from birds, 83 from lizards, 96 from rodents and 11 from wasps. Multinomial logistical regression predicted the model with 72% accuracy and a Kappa value of 0.53 and this was used to determine significance (Table 6.1).

Table 6.1: State (burnt or unburnt), model type preference (control or spider) and size (large or small), and frequency of predation by identified predator type (bird, lizard, rodent or wasp). Of the 1200 models used in the experiment, 109 were excluded from analysis for various reason, including but not limited to: melting, unable to re-locate or stolen. Multinomial logistic regression was used to determine significance *: p < 0.05, **: p < 0.01, ***: p < 0.001, and ****: p < 0.0001 within column categories: state, model type and model size.

	State		Model type		Model size	
	Burnt	Unburnt	Spider	Control	Large	Small
Birds	163**	73	79	157*	127	109
Lizards	44	39	60	23	52	31
Rodents	36	60**	78*	18	51	45
Wasps	2	9***	11****	0	6	5

Predation was higher in burnt than in unburnt patches for birds, but with no preference for spider models (Table 6.1). Preference for spider models over controls was significant for rodents, and they also predated significantly more in unburnt areas (Table 6.1). Wasps predated exclusively on spider models and significantly more in unburnt patches, but low samples sizes could be yielding type I errors (Table 6.1).

The twenty-four site-state-model units clustered into five distinct groups, each based largely on a single predator type (Figure 6.2).

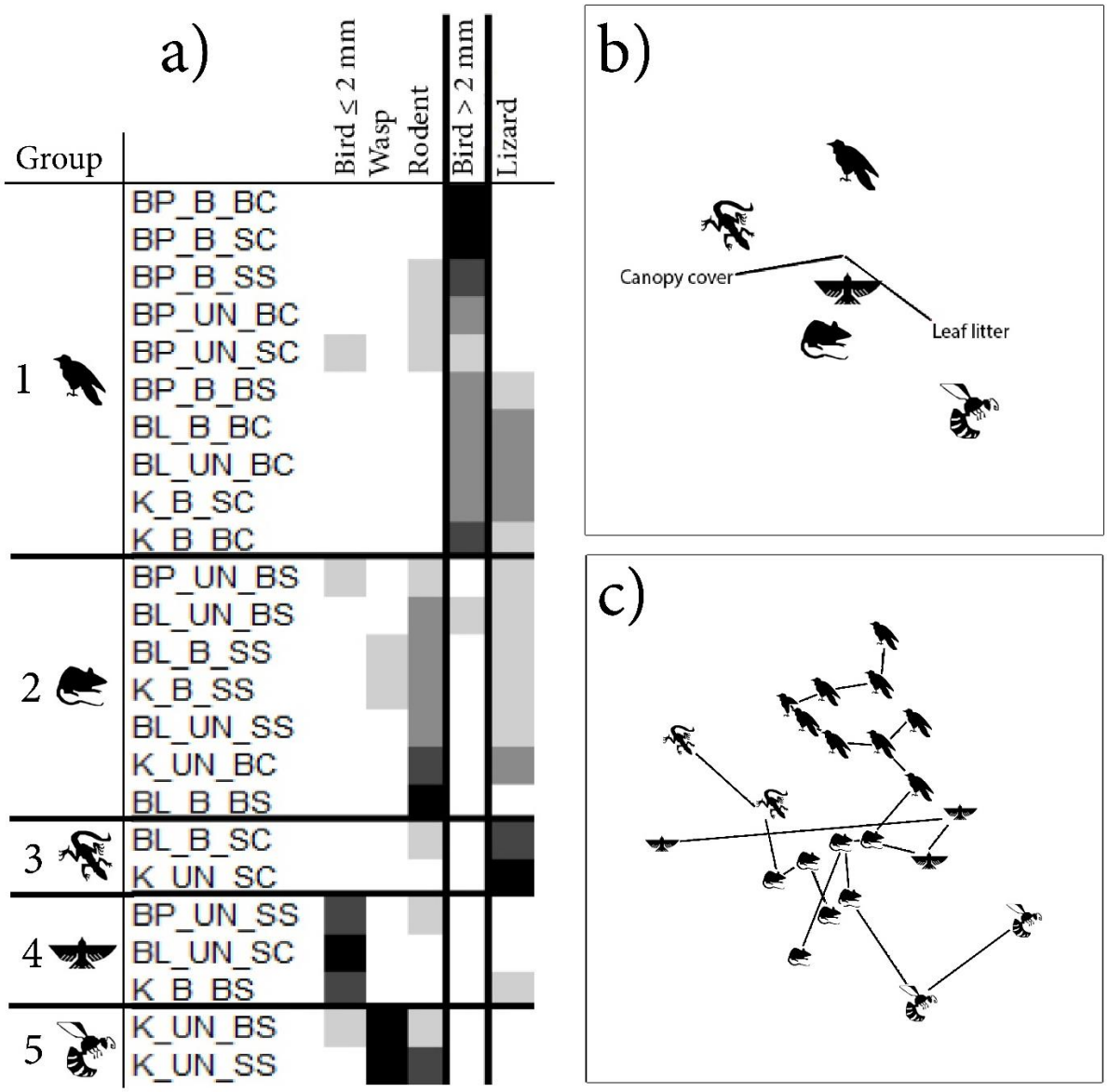


Figure 6.2: 2D semi-strong hybrid (SSH) multidimensional scaling (MDS) ordination (Stress: 0.15) based on twenty-four site-state-model units and five predation types (Gower Metric Association Measure, Classification Strategy: Agglomerative Hierarchical Fusion, Technique: Flexible UPGMA). Predation types were used as intrinsic factors and combined site, state and model type were used as extrinsic factors in numerical taxonomic analysis. Site, state and model type units are in codes in the two-way table. The first line refers to the site of urban bushland and corresponds to the site map (BP, BL and K; Figure 2), the second line of text refers to state (UN: unburnt and B: burnt) and the third line of codes refers to model type (BS: 5 mm spider, BC: 5 mm control, SS: 3 mm spider and SC: 3 mm control). a) Two-way table. b) Extrinsic factors canopy (p value: 0.03) and leaf litter cover (p value: 0.02) were significantly correlated. c) Five distinct groups emerged based on dominant predation type; Bird ≤ 2mm (), wasps (), rodents (), birds > 2 mm () and lizards ().

Group 1 included ten site-state-model units based on predation by large birds at Bold Park. Group 2 has seven site-state-model units, mostly based on high rodent predation. Group 3 consisted of two site-state-model units with high lizard predation. Group 4 formed a cluster based on three site-state-model units with high bird (> 2 mm) predation. Group 5 included two site-state-model units based mostly on wasp predation at Kensington on spider models in unburnt areas. Two

extrinsic variables; leaf litter cover and canopy cover were significantly ($p = 0.02, 0.03$ respectively) correlated with the ordination axes.

6.7 Discussion

6.7.1 Burrow survival

Our study suggests that high intensity fires are a severe threat to mygalomorph populations in urban remnant vegetation. However, the percentage of mygalomorphs surviving a low intensity fire is high. Reasons for post-fire mortality are unknown, but three burrows were invaded by ants and sixteen by wasps. When excavating the burrows, evidence of wasp predation was apparent through hatched or defunct cocoons, but it remains unknown how this compares to the natural rates of wasp predation.

Based on similar burrow diameters and structure, 18 spiders re-located a short distance (all less than 1.5 m) away from their original burrows rather than re-lining their original burrow. This was noted at Kings Park as the existing leaf litter made burrows with twig-lining arrangements obvious. It is unknown whether this was also occurring at Shenton Park Field station. There, no leaf litter remained due to the high intensity of the fire. If spiders were relocating post-fire at Shenton Park, the heavy ash beds may have obscured new burrow entrances. Therefore, it is possible that survival was higher than recorded.

Recovery of other invertebrate species is likely to occur at a greater rate after low intensity rather than high intensity fires, perhaps due to the retention of some resources and rapid recovery of vegetation (Malmström 2006; Verma and Jayakumar 2012). Recovery of other invertebrate species may determine survivorship of mygalomorphs. Survivorship of mygalomorphs was high in prescribed (low-intensity) burn experiments that investigated changes in spider assemblages post-fire at Lorna Glen Station (Langlands *et al.* 2011) in the arid-zone of Western Australia. However, overall species diversity may be compromised if low-intensity prescribed burning occurs too often (Springett 1976; York 1999) or becomes too intense due to increased fuel load from weeds (Fisher *et al.* 2009).

Weed invasion, particularly veldt grass (*Ehrharta* sp.*)*, is detrimental to mygalomorph spiders' survival (Mason*,* Bateman, and Wardell-Johnson 2018) and to biodiversity (Fisher *et al.* 2009) in Perth. In this study we found comparatively few trapdoor spider burrows in veldt grass dominated areas (Bold Park, $n = 2$) compared to a similar area in weed-managed habitat (Kings Park, $n =$

103) surveyed after burning. This finding further supports understanding of the detrimental impact of veldt grass on urban mygalomorph populations (Mason, Bateman, and Wardell-Johnson 2018).

6.7.2 Predation

Bird predation was higher in burnt than in unburnt patches, but with no preference for spider models, perhaps indicating opportunistic foraging in burnt areas. Preference for spider models over controls was shown in rodents and wasps but both were predated significantly more in unburnt areas. This suggests that their behaviour may not be related to post-fire conditions, possibly attributable to the lower leaf-litter cover, understorey cover and canopy cover in these sites (Mason *et al.* 2018).

Indeed, predation behaviour is strongly correlated with canopy cover and leaf litter (Figure 6.2b, Mason *et al.* 2018), rather than in response to fire. As only large birds significantly changed their predation behaviour in response to fire, high mobility may be conducive to opportunistic post-fire foraging. Only two predator types, rodents and wasps, indicated preference for spider models over controls but this was seemingly unrelated to fire (Mason *et al.* 2018). Indeed, some wasps are spider-specialists so it is unlikely that fire would impact their foraging behaviour in this way, except perhaps if the fire destroyed the lair to which they drag paralysed spiders (Evans and Matthews 1973, Mason *et al.* 2018). We suggest that control models always be included in clay model predation studies to avoid Type 1 errors and to provide greater insight into predator behaviour (Bateman, Fleming, and Wolfe 2017, Mason *et al.* 2018).

6.7.3 Conservation implications

Fires in urban areas are particularly detrimental to low-mobility taxa as those able to escape fires may lose access to suitable habitat. The bushland remnants in this study were large enough and sufficiently accessible for fire response teams to extinguish the flames before the entire patch was burnt. Unfortunately, this outcome is not always achievable in smaller reserves in more recently urbanised and isolated areas of Perth. Small, isolated patches of bushland have high biodiversity value due to the landscape effect and the hosting of endemic local species (Fahrig 2003). For SREs, these small patches may be the last remaining refuge for these species. Fire from arson may also be more common in small patches throughout newer suburbs due to societal factors (Willis and Territory 2004). As high fines for arson seem ineffective, damage may sometimes be mitigated by using low-intensity burns to reduce fuel loads.

Fine litter fuels in Banksia woodlands without grassy weeds accumulate through time to plateau at around 6 years after fire (Burrows and McCaw 1990). Where grassy weeds are present, fine fuels may accumulate more rapidly, attaining higher levels and continuity than non-invaded remnants (Fisher *et al.* 2009). An average of 3,300 fires known or suspected to be caused by arson, or other human activity (i.e. accidental) comprised between 30% and 55% of the 31,271 fires reported in the Perth region between 2004 and 2012 (a further 13% were 'unknown cause') (Plucinski 2014).

6.7.4 Management recommendations

One approach to maximising biodiversity is for fire management regimes to attempt to match the natural fire regimes of the relevant area. However, identifying a natural fire regime is problematic for much of Australia (Miller and Murphy 2017). For example, pre-European fire regimes are poorly known for Banksia woodlands. Regardless, the summer drought of this Mediterranean climate area makes wildfire most likely in the late summer and autumn.

Mygalomorph spiders are highly seasonal in their mating and dispersal events (Main 1984; Mason *et al.* 2018). The fraction of males roaming at any time in a certain area is predictable due to their tendency to emerge during peaks in high relative humidity or rain. In Perth, this may indicate an evolved strategy in mygalomorph species that males roam between April and August to mitigate fire risk (Mason *et al.* 2018). March and February have low records of male activity (Mason *et al.* 2018). Males of a species may emerge earlier or later than the majority, meaning if a fire does occur, not all males will be killed. Therefore, the likelihood of some being killed in an April prescribed fire is a worthwhile trade-off for the persistence of other taxa contributing to biodiversity in urban areas.

Disturbances such as high intensity burns, which suggests that August to be an optimal time for burning for mygalomorph management. However, August is the least likely time for burning under natural regimes, would often be practically difficult to execute, and is potentially hazardous for other flora and fauna.

Fires are inconvenient and dangerous for residents of urban areas (Gill and Stephens 2009; Solangaarachchi, Griffin, and Doherty 2012). In an urban context, natural behavior of taxa may change contextually (Abbott 1984; York 1999). Opportunity to escape to adjoining habitat for some species may be low and those that cannot escape may be exposed to novel subsequent threats (weed invasion, predation). A low-frequency, mosaic or patchy burning approach that does not

reduce heterogeneity over time (Fox and Fox 1986; Nieuwenhuis 1987) and encourages high rates of recovery is recommended for mygalomorphs. This approach may allow for low mobility or sedentary species to persist. Patchy burning with an experimental approach is recommended for small bushland reserves (< 5 ha) in densely populated areas, as these are also prone to weed invasion – potentially a greater threatening process for SREs. As burning encourages weed establishment, subsequent weed management through weed spraying post-fire may be more cost-effective.

Future research priorities include determining fire response to enable management for a suite of species with relevant characteristics, to determine and mitigate immediate and/or subsequent threatening processes.

Chapter 7

General Discussion

"If there is anything in the universe that can't stand discussion, let it crack."

~ Wendell Phillips (1811 – 1884)

7 General Discussion

7.1. Thesis synthesis

This invertebrate conservation study assessed threatening processes that may affect the presence and persistence of mygalomorph spiders in 42 discrete patches of urban vegetation remnants in Perth, south-western Australia. Mygalomorph spiders were used as surrogates of 'short-range endemics' i.e. taxa with shared traits of low dispersal capacity, low mobility, low fecundity and with an entire distribution within 10 000 km^2. **Chapter 2** aimed to contextualise mygalomorphs and other SREs in relation to other types of life investment. The main objective of this chapter was to emphasise the need for conservation to move away from traditional ideas involving a taxonomic approach where single species are assessed and prioritised. It is simply not appropriate to use such an approach for the vast majority of invertebrate clades. Instead, understanding functional traits that are susceptible to identified threats will allow an unbiased assessment of species for prioritisation. While threats must be assessed contextually, the response of functional traits may be globally applicable. Here, the functional traits (represented in mygalomorph spiders as surrogates for other SREs or *groovers*) response to threats present in an urban context was assessed locally, but may be applied globally. For example, **Chapter 3** quantified whether the quality of habitat was more important in determining presence or absence of mygalomorphs than was the quantity of habitat. I found that quality of urban vegetation remnants was significantly positively correlated with the presence of mygalomorph spiders, but quantity of habitat was not; perhaps in response to their sedentary nature as a functional trait. **Chapter 4** confirmed microhabitat specialisation and some degree of choice during dispersal as functional traits for mygalomorph spider species. The implication of specialisation in heterogenous habitats that are becoming homogenised, is that such homogenising processes (such as invasion by non-native grasses) are a high-impact threat on such traits. To investigate the cryptic threat of predators in an urban context and better understand species-specific threats that may differ based on phenological traits, I quantified attacks on mygalomorph spiders, that may vary with size and mating phenologies, using clay models in **Chapter 5**. I found that spider models were significantly preferred by all predator types, but that a significant majority of wasp attacks occurred in summer and exclusively on spiders. This means wasps may only pose a threat to *Aname* males in Perth. However, as wasps are specialised native predators with populations dependant on their prey species, I concluded that wasps were unlikely to be a significant threat when compared with invasives (e.g. rodents) or native predators with unnaturally higher abundances in urban areas (e.g. corvids). In **Chapter 6** I found that predation rates on spiders were higher in burnt than in unburnt areas, fire as a threat may

continue until vegetation can recover. This means that those SREs able to survive the fire itself, may not survive the post-fire environment. Intense fires in urban remnants are especially threatening to taxa with low mobility and dispersal functional traits. Mygalomorphs typically dig burrows and therefore may be expected to be buffered from the effects of burning vegetation during a fire, so this trait may offset what may be a typical response in other SREs.

When combined with extensive habitat clearing, the threats investigated here may be considered adequate to afford official protections for mygalomorphs (and other SREs that share functional traits) in urban areas of Perth. These threats can be summarised in Figure 7.1.

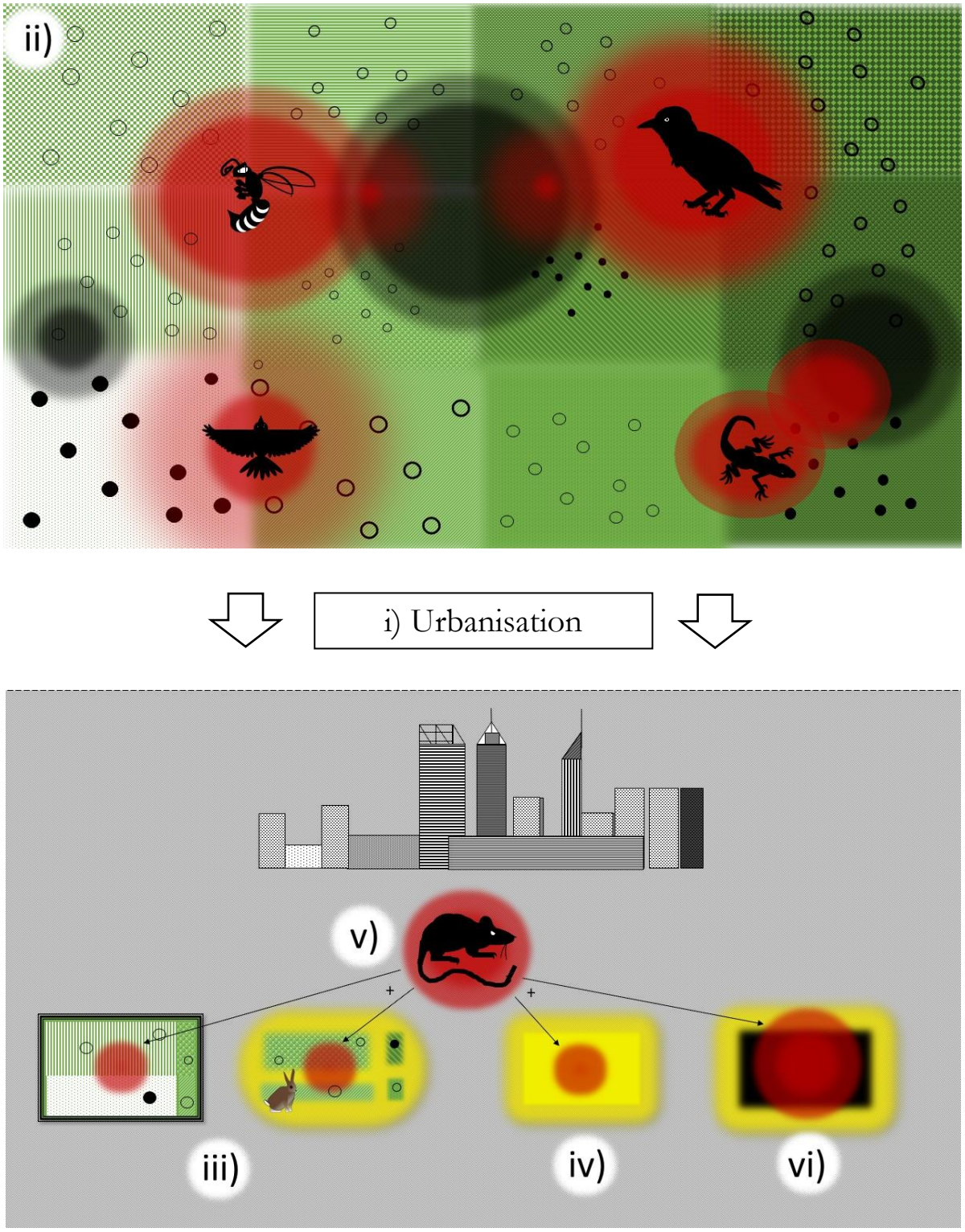


Figure 7.1: i) Urbanisation (human populations becoming centralised) has been occurring on the Swan Coastal Plain since being founded in 1829. ii) Historically, the Swan Coastal Plain - upon which Perth urban extent is now sprawling - was highly heterogeneous and inhabited by many *groovers* (circles) specialising in different microhabitats (green patches). Natural threats such as fire (black) and attacks by different (icons) predators (red) would be present. iii) Quality of remaining habitat can be maintained through management of invasive grass and rabbits. iv) Invasive grass (yellow) can become a homogenising force – removing required microhabitats. v) Invasive predators may cause increased pressure on already threatened populations. vi) Fire has the compacity to extinguish populations and promote secondary threats such as increased predation and invasive weed.

7.2 Conservation management implications

A combination of lack of concern and inadequate understanding of SRE conservation has resulted in insufficient funding and conservation outcomes. This is concerning as SRE clades represent some of the largest contributors to biodiversity (Harvey *et al.* 2011). A lack of resources for invertebrate research means that many species will go extinct without our protection or knowledge. A greater investment into research on feasible and effective SRE conservation outcomes would offer future returns on species recovery and persistence.

Conservation of SRE species is a challenging task as it is complex and involves many aspects worthy of consideration that, without more information, are difficult to prioritise. Many invertebrate species, and perhaps especially SRE taxa, may be considered 'data deficient' for IUCN red listing. In **Chapter 2,** I have advocated a need for change in such a system to allow for protection of species based on their functional traits and threats. Many mygalomorph species extent of occurrence is restricted to the already severely fragmented habitat with Perth urban extent, meaning the area of occupancy is dramatically reduced. In **Chapter 3**, I discussed the need for adequate management against degrading forces such as invasive grass and rabbits. **Chapter 4** emphasises the extreme threat of unmanaged invasive grass to urban fragments – causing local extinctions within homogenised patches. **Chapter 5** investigates a cryptic threat of predators attacking males during breeding season, that in an urban context may further endanger already dwindling populations. **Chapter 6** considers fire as a major threat to any taxa that has low mobility and dispersal, and especially a threat to mygalomorph spiders when combined with secondary fire effects such as invasive grass and increased predator activity. Based on the findings in this thesis I would recommend that all species of mygalomorph, and perhaps other SREs restricted to the urban extent of Perth, to be afforded some official level of protection. At the very least, an IUCN red listing of 'Vulnerable' would be applicable. For species where the only records exist within Perth urban extent or on the Swan Coastal Plain (such as *Idiosoma sigillatum*), as high as 'Critically endangered' may be asserted. Indeed, it is likely that many species have already gone extinct with or without documentation of their existence.

Overall, this thesis reveals an effective approach to improve understanding of current conservation concerns for mygalomorph spiders and other SREs in urban areas. Solutions for problems in conserving SRE species that I present here and throughout my thesis are by no means comprehensive, but may be widely applicable. Conservation of SRE species will require ongoing,

in-depth research in a variety of different contexts. Globally, estimation of extinction risk in rapidly changing environments is impossible without such research.

7.3 Assumptions and model limitations

One of the major assumptions that I make throughout my thesis is that conclusions drawn from my research on mygalomorph spiders will also be broadly applicable to other SREs. While this may be a valid assumption for **Chapters 3** and **4**, the burrowing behaviour of mygalomorph spiders and local phenology means that findings in **Chapter 5** and **6** respectively should be viewed contextually. Indeed, further research into SRE species should include traits relevant to persistence for specified threatening processes. For example, mygalomorph spiders readily survive low intensity fires (**Chapter 5**), but the same may not be true for snails, millipedes and other typically SRE taxa. Similarly, phenology (**Chapter 6**) may be differentially influenced for many invertebrate taxa - not just SREs - under our currently changing global climate (Walther *et al.* 2002).

Another major assumption is that all mygalomorph spider species I studied throughout my thesis are, in fact, SREs. It is difficult to quantify standard measures to classify species as SREs, with total distribution being only one approach (Harvey 2002; Harvey *et al.* 2011). Classification of SRE species is problematic as sufficient surveying needs to be undertaken to justify classification as anything other than 'data deficient' (Gasc *et al.* 2013). Lack of classification due to data deficiency is an ongoing issue for all invertebrate conservation (Braby in press). Recently, genetic testing has allowed better understanding of mygalomorph lineages, though species level is still difficult to quantify. Genetic testing should be used to further delineate species as this has high implication for classification of conservation priorities, but rarely implemented due to monetary expense. Further, (and as implied in **Chapter 2**) all life histories vary based on space, time and resources. It may be that for any progress in SRE conservation studies - where time, effort and resources are limited - some assumptions must be made before species are lost to extinction.

7.4 Future directions

My thesis heavily emphasises the need for SRE conservation and how this may be applied; however, it is not prescriptive for practical implementation. Rather, my thesis is intended to provide an example of how SRE species can be incorporated into conservation research. Implementation of conservation strategies will be heavily influenced by contextual elements such as local culture, politics and existing frameworks. Conversely, threatening processes may be similar

for SREs globally, as their traits may indicate. I allude to this idea in **Chapter 2,** where various taxa are broadly grouped as *boomers* (high reproductive output but low mobility and specialisation), *groovers* (high specialisation but low mobility and reproductive output) and *movers* (high mobility but low reproductive output and specialisation) based on investments in future, place and self respectively. Due to shared traits of groups, future studies could focus on how various threatening processes may affect these groups to varying extents. For example, *groovers* (of which SRE species are an extreme example) may be more greatly affected by invasive species, homogenising processes or other disturbances more so than other groups. Conversely, *movers* (such as migratory species) may be more threatened by a lack of global policy that protects essential habitats but not be as affected by invasive species or such disturbances in their habitat(s).

Invasive species were found to be a major threatening process for mygalomorph spiders, and other SREs, throughout Perth in **Chapter 3**. A future direction could be to compare urban taxa with taxa from more intact, natural habitat to assess what traits may enable persistence in urban areas. By contrasting available resources, time and space variables with traits of those occurring naturally and those that persist in the urban environment it may be possible to predict persistence. If we can predict responses, then we should be able to better accommodate taxa or at least mitigate harmful effects.

Comparison of original to novel circumstances could also be applied to invasive species. In **Chapter 4**, I found invasive veldt grass to be a major threatening process. Comparison of invertebrate assemblages between naturally occurring veldt grass in its place of origin (South Africa) to invertebrate assemblages in invaded systems (Perth, Western Australia) would provide insight to the effective functioning traits of the veldt grass ecotype. Those invertebrate species that can survive in invaded areas would likely have similar traits to those found in the original habitat. By determining what persisting traits correlate, we can better predict the loss of biodiversity induced by invasive species. Veldt grass also poisons native plants by accumulating K in the soil that they cannot cope with in large amount. It is not yet known how soil chemistry may impact on mygalomorph spiders in Perth, but it is certainly worth considering for future studies (especially in relation to fertilisers, weed killers and salinity).

Similarly, recovery of invertebrate assemblages in post-fire conditions would be heavily influenced by possessing certain traits. The findings of **Chapter 5** could be greatly enhanced in future by tracking invertebrate assemblages over time in different patches that vary in time, space and resources. Urban patches of vegetation are often isolated and vary in size. Determining mobility, reproductive out and specialisation traits of current patch occupants, and how this may influence

their initial response, persistence and natural re-colonisation of patches post-fire. This will assist with fire management in urban areas.

Predator assemblages in urban areas, such as those recorded in **Chapter 6**, are indicative of what traits may enable persistence. Unfortunately, changing predator assemblages will also drive a top down change on prey species – representing a cryptic threatening process. To better understand how predators adapt to urban environments and the varying impacts this will have on their prey, future experiments could provide a range of different shapes, colours and movement (rather than models remaining stationary) for clay models. Repetition of experiments, or collection of data within smaller time frames may also provide insight to differences in predator learning.

For mygalomorph spiders specifically, there are multiple areas worthy of further investigation. Recently, the shield-backed trapdoor spider (*Idiosoma nigrum*) clade was genetically assessed. The only spider species in Australia to be protected under state and federal legislation is *Idiosoma nigrum,* though two sister species *I. formosum* and *I. kopejtkaorum* are protected under state law (Rix et al. 2018). However, confusion of subsequent conservation status arises when a protected species is divided. It is highly likely that genetics studies will continue to split currently recognised and described mygalomorph species into multiple species, so the question of conservation status is relevant, if poignant. I find it distressing that the status of protection was only retained for *Idiosoma* species previously described. Logic would follow that if the species was considered endangered before this genetic analysis, the division of its known populations into different species would no doubt increase the threatened status of all concerned, not remove it entirely. This needs to be immediately addressed, as lifted protection means threats such as clearance associated with mining can, and will proceed. This is not to undermine the importance of genetic studies, only highlight the that consequences are potentially undermining conservation efforts and appropriate protocol must be constructed to be implemented following such genetic studies.

Indeed, one of the studies I intended to include in my thesis was a genetic study; retrieving eDNA from the silk-lining of mygalomorph burrows as a non-invasive approach of species identification. Unfortunately, molecular markers needed to be developed to complete this study and it was on my expertise and time restrictions imposed. This would be a rewarding post-graduate study.

Conservation of mygalomorph spiders does not only benefit biodiversity and intrinsic values. Other benefits include, but not limited to; medical advances, agricultural application and ecotourism. For example, mygalomorph spider venom derivatives have been used for post-stroke treatment (King 2011) and targeted insecticides (King and Hardy 2013). Venom is species specific,

and in future studies may be collected, along with genetic material, to enhance our understandings of species delineation. Regardless, current studies suggest venom is species-specific, and there will undoubtedly be heavy investment by industry towards venom acquisition in the future for human benefits. My concern is that exploited species will receive no benefits for an otherwise one-way transaction, with no associated tax. Future directions in this area could develop policies pertaining to, and taxing industry when using biological derivatives (for services rendered) and for which proceeds could then be used for species conservation. Such a policy would likely be well received by the public as it encompasses many intrinsic and economic values. However, governments would undoubtedly prefer that any 'goods from species' taxes be returned to the state or nation to be used at their discretion. Discretion that may or may not relate to conservation management of the exploited species. My suggestion to future policy makers and government, is to state explicitly what percentage of such a tax will go towards directly benefiting the exploited species and their conservation.

Overall, short-range endemism is a global phenomenon, findings are often widely applicable, and we must make a worldwide effort to preserve these species. Unfortunately, the current state of SRE conservation means that efforts may be too little too late for many species. It is therefore imperative that we prioritise SRE research to save the rich biodiversity that is still represented. We must advocate SRE conservation as an investment in the future of our planet, not only in terms of environmental benefits, but benefits to humanity. A lack of advocacy is considered one of the major impediments to invertebrate conservation outcomes (Braby in press). Although still not widely implemented, science communication for SRE conservation may assist with advocacy problems. To provide effective science communication, it is especially important to consider various cultural and social perspectives. To capture the concern of people less environmentally inclined, effective science communication may include benefits to humanity that mygalomorph spiders and other SRE taxa may provide.

7.5 Final words

My thesis offers insight into the threatening processes relevant to a highly under-researched clade. I have provided novel findings that will enable more informed conservation practises. However, there is still a great deal of research that needs to be completed before we have a comprehensive understanding of such cryptic creatures and management practises become mainstream. It is my hope that future generations will have an opportunity to experience similar joy and intrigue I continue to find in mygalomorph spiders.

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9 Appendices

9.1 Appendix: Table of trait values used for PATN analysis in Figure 2.1

#	Scientific name	Common name	Broodsize	Dispersal	Migration	Activity	Responsive	Specialisation	References
1	*Moggridgea tingle*	Trapdoor spider	40	0	0	0	0	1	(Cooper *et al.* 2011)
2	*Hoggicosa bicolour*	Wolf spider	30	0.3	0	0.5	0.5	0	(Langlands and Framenau 2010)
3	*Neriene litigiosa*	Sheet weavers	37	0.9	0	0	0.9	0.25	(Watson 1998)
4	*Tetragnatha extensa*	Long-jawed spiders	65	0.9	0	0	0.9	0.5	(Greenstone *et al.* 1987; West and Toft, 1999)
5	*Tetragnatha restricta*	Long-jawed spiders	65	0.2	0	0	0.1	0.5	(Gillespie 2005a, 2005b)
6	*Cherax quinquecarintus*	Gilgie	76	0.5	0	0.1	0.1	0.25	(Beatty 2005)
7	*Cherax cainii*	Smooth marron	286	0.5	0	0.1	0.1	0.35	(Beatty 2005)
8	*Cherax pallidus*	Indonesia freshwater crayfish	100	0.1	0.1	0.1	0.1	0.5	(IUCN 2018)
9	*Synalpheus realis*	Snapping shrimp	5000	0	0	0	0	1	(Duffy *et al.* 2002)
10	*Penaeus monodon*	Tiger prawn	750000	0.9	1	0.9	0.8	0	(Kungvankij *et al.* 1989)
11	*Drosophila melanogaster*	Fruit fly	500	0	0	1	1	0	(Jenkins *et al.* 2013; Schmidt *et al.* 2005)
12	*Drosophila hawaiian*	Fruit fly	500	0	0	1	1	1	(Kaneshiro and Boake 1987)
13	*Danaus plexippus*	Monarch butterflies	500	0	1	0.5	0.5	0.25	(Field 2013; Johnson 1969; Urquhart 1960)
14	*Oreixenica latialis theddora*	Small alpine xenica	500	0	0	0	0	0.95	(New 2008)
15	*Semibalanus balanoides*	Acron barnacle	10000	1	0	0	0	0	(Kordas and Dudgeon 2009; Southward 1987)
16	*Euphausia pacifica*	North Pacific Krill	4500	1	1	1	1	0	(Gómez-Gutiérrez *et al.* 2006)
17	*Diadema antillarum*	Sea urchin	1000000	1	0	0.3	0.3	0.2	(Garrido *et al.* 2000; Levitan 1991)
18	*Chortoicetes terminifera*	Australian plague locust	70	1	1	1	1	0	(Hansen *et al.* 2011)
19	*Phalangacris alluaudi*	Mahé boulder cricket	70	0	0	0	0.1	0.5	(IUCN 2018)
20	*Dryococelus australis*	Lord Howe stick insect	300	0	0	0	0.1	1	(IUCN 2018)
21	*Hirudo medicinalis*	Medicinal leech	50	0.1	0	0.9	0.1	0.5	(IUCN 2018)
22	*Perionychella ngakawau*	New Zealand earthworm	20	0	0	0	0	0.5	(IUCN 2018)
23	*Lumbricus terrestris*	Common earthworm	20	0	0	0	1	0.5	(Frelich *et al.* 2006)
24	*Necator americanus*	Hookworm	300000	1	0	0.1	0.1	0.5	(Hotez *et al.* 2005)
25	*Linepithema humile*	Argentine ant	172800	0	0.4	0.5	0	0.25	(Markin 1970; Menke *et al.* 2018)
26	*Nothomyrmecia macrops*	Dinosaur ant	10000	0	0.1	0.1	0	0.75	(IUCN 2018)
27	*Cryptotermes brevis*	Powderpost termite	10000	0	1	1	0	0.25	(Roisin 2000)
28	*Rhinella marina*	Cane toad	50000	0.4	0.5	0.9	0.1	0	(Shine 2010)
29	*Spicospina flammocaerulea*	Aussie sunset frog	80	0	0	0	0.1	0.5	(Dziminski and Anstis 2004)
30	*Alytes obstetricans*	Common midwife toad	150	0.3	0	0.1	0.1	0.25	(Márquez *et al.*1997)
31	*Mola mola*	Sunfish	300000000	1	0	1	0.6	0	(Cartamil and Lowe 2004; IUCN 2018)
32	*Salmo solar*	Salmon	1000	1	1	0.9	0.8	0.05	(Fleming 1996)
33	*Psychrolutes marcidus*	Blobfish	1000	0	0	0	0	0.4	(Collins *et al.* 2006)
34	*Hippocampus capensis*	Seahorse	350	0.1	0	0.1	0.1	0.8	(IUCN 2018)
35	*Chelonia mydas*	Green sea turtle	150	0.6	0.5	0.9	0.1	0.15	(Goshe 2009)
36	*Caretta caretta*	Loggerhead turtle	150	0.6	0.5	0.9	0.1	0.45	(Broderick *et al.* 2003)
37	*Pogona vitticeps*	Central bearded dragon	120	0.2	0.1	0.4	1	0.5	(Swan 2008)
38	*Typhlosaurus gariepensis*	Lomi's Blind Legless Skink	1	0	0	0	0	1	(Huey *et al.* 1974; IUCN 2018)
39	*Geospiza septentrionalis*	Vampire finch	3	0	0	0.1	0.5	0.75	(Farrington *et al.* 2014; IUCN 2018)
40	*Branta canadensis*	Canadian Goose	7	0	1	0.3	0.3	0.1	(Mowbray *et al.* 2002)
41	*Cuculus canorus*	Common cuckoo	50	0.8	0.2	0.5	0.7	0.5	(Rutila *et al.* 2002)
42	*Ailuropoda melanoleuca*	Panda	0.5	0	0	0.2	0.1	0.6	(Charlton *et al.* 2009; IUCN 2018)
43	*Balaenoptera bonaerensis*	Antarctic minke whale	1	0	1	1	0.2	0.05	(Bombosch *et al.* 2014)
44	*Oryctolagus cuniculus*	European rabbit	7	0.2	0	0.6	0.9	0.05	(Lombardi *et al.* 2003)
45	*Pteropus tuberculatus*	Vanikoro flying fox	1	0	0	0.1	0	0.5	(IUCN 2018)
46	*Pteropus alecto*	Black flying fox	1	0	0	0.9	0.9	0.1	(Vardon and Tidemann 1998)
47	*Heterocephalus glaber*	Naked mole-rat	11	0	0	0.1	0.1	1	(Sherman and Jarvis 2002)

9.2 Appendix: References for Appendix 9.1

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